D. Elmo Hardy Memorial Volume

Contributions to the Systematics and Evolution of Diptera

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Contributions to the Systematics and Evolution of Diptera

Edited by
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Bishop Museum Bulletin in Entomology 12

Bishop Museum Press
Honolulu, 2004

Published by
Bishop Museum Press
1525 Bernice Street
Honolulu, Hawai‘i 96817-2704, USA

Printed in the United States of America

ISBN 1-58178-022-2
ISSN 0893-3146

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PREFACE

D. Elmo Hardy, "one of the last polymaths of Diptera Systematics" (see Evenhuis' "Biography of D. Elmo Hardy", this volume), died on 17 October 2002. Elmo, as he was known to most who knew him personally, was not only a dipterist extraordinaire, he was a teacher and mentor to students of entomology throughout the Asia-Pacific Region. Over the nearly seven decades of active research, Elmo named and described nearly 2,000 species in 34 different families of Diptera. These were published in 437 articles and notes (see Evenhuis & Thompson, this volume). Elmo may be considered the "father of Hawaiian Dipterology" and has inspired the research of many students of Diptera systematics. The collection of articles in this volume is a celebration of Elmo's achievements in the taxonomy and systematics of flies from the Asia-Pacific Region.

Evenhuis' lead article on the Biography of D. Elmo Hardy is a narrative of Elmo's personal life as well as his scientific career. The primary reference for the article is an unpublished autobiography and is full of personal stories about his childhood years, his many travels to exotic parts of the world, and insights into his formative years that led to his interests in insect systematics.

The article by Skevington and DeMeyer describes Elmo's contributions to the systematics of Pipunculidae, or big-headed flies. Bickel, in his article, describes a new genus of Dolichopodidae and names the type species for this genus, *Alishania elmohardyi*, in recognition of Elmo's work on the taxonomy of this family of flies. This is followed by Evenhuis' article describing another new genus, *Humongochela*, in the family Dolichopodidae.

The Kaneshiro paper is a review of his earlier work on the behavioral genetics of the Hawaiian Drosophilidae in understanding the role of sexual selection in the formation of new species in this group. Uechi et al. presents a description of host alternation in species of gall midges in the genus *Asphondylia*. They present evidence from DNA analyses that *A. gennadii* can complete its life cycle by utilizing at least four different host plants alternatively.

Norrbom and Hancock describe three new species and six new records of Tephritidae increasing the total number of species from New Caledonia from 16 to 25. Fitzgerald discusses five species of Bibionidae from New Caledonia, four of which are described as new species. Mathis & Zatwarnicki present a revision of five species in the shore-fly genus *Trimerogastra* of which two are described as new species.

Carson's paper is a review of his earlier studies on the use of inversion patterns in the giant polytene chromosomes as "tracers" of phylogenetic relationships among 107 species of picture-winged Hawaiian drosophilids. He also discusses the role of sexual selection in species formation.

The O'Grady & Silvestri paper presents some new DNA data and, together with morphological and behavioral data, the authors infer phylogenetic relationships among the fungus-feeder group of species in the endemic Hawaiian drosophilids. The authors provide evidence that some of the species group relationships based on morphological data alone need to be revised when the molecular data are incorporated.

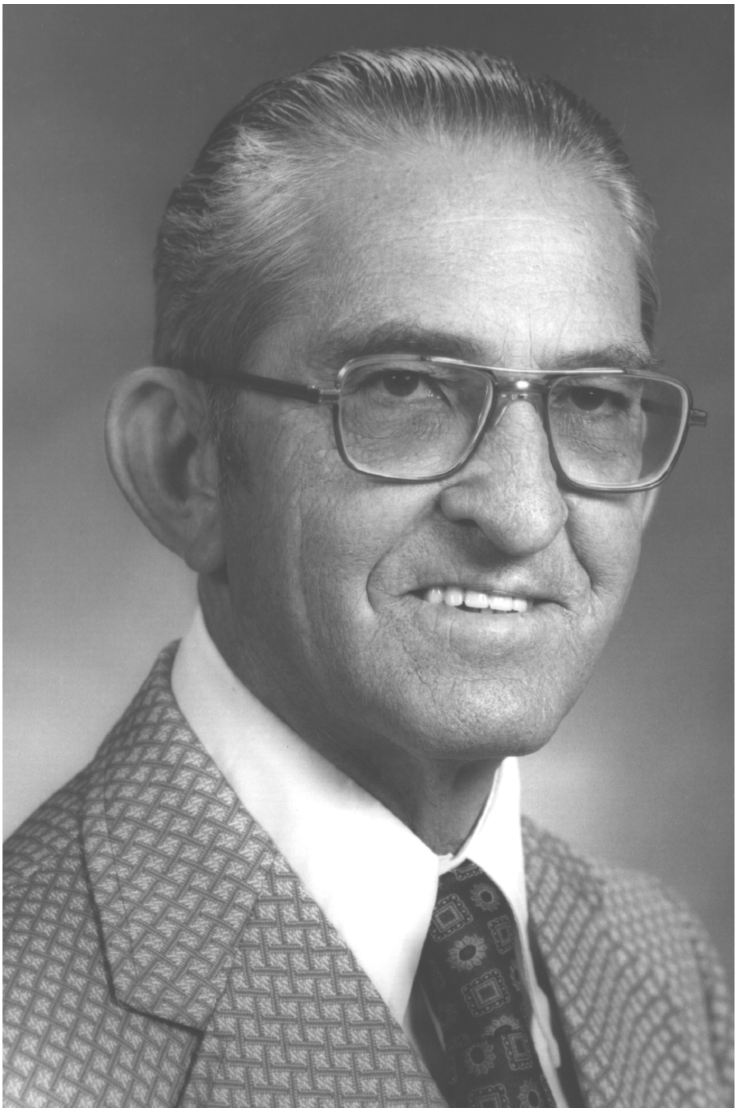
Copeland *et al*. report on insect host associations of Oleaceae in Kenya. They sample four genera (13 species) of the olive family and reared five species of tephritids, including one new species, as well as four braconid parasitoids that were reared from the pupae of these tephritids. They also report on the lepidopteran species and their parasites that were reared from the fruit samples.

Drew presents a discussion of the biogeography and speciation in the Dacini group of Tephritidae, primarily of species in the genera *Bactrocera* and *Dacus*. He suggests that the close relationship between these fruit fly species and its host plant where courtship and mating occurs has had a significant influence on the speciation process and the evolution of this group of flies.

The final chapter is a complete list of Elmo's publications and of dipteran taxa he described. These include 437 articles and notes where 1,867 species in 34 families of Diptera were treated.

This volume would not have been possible without the willingness and enthusiasm of each of the contributors. We are also indebted to those who reviewed and critiqued the manuscripts; their critical comments and suggestions significantly enhanced the quality of this volume.

N.L.E.
K.Y.K.
Honolulu, Hawai‘i
January 2004



D. Elmo Hardy Memorial Volume. Contributions to the Systematics and Evolution of Diptera. Edited by N.L. Evenhuis & K.Y. Kaneshiro.
Bishop Museum Bulletin in Entomology 12: 1–11 (2004).

Biography of D. Elmo Hardy
(1914-2002)[1]

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Introduction

D. Elmo Hardy, "Elmo" to all who knew him personally, was one of the last polymaths in Diptera systematics. His knowledge of Diptera families spanned the order from Nematocera (specializing in Bibionidae), through to the Brachycera (specializing in the families Pipunculidae, Drosophilidae, and Tephritidae). He expanded his knowledge of the systematics to many other Diptera families through his monumental efforts in producing 5 volumes of Diptera for the "*Insects of Hawaii*" series where he described 581 species in no less than 20 families in the 30 years it took to conduct that research and produce those volumes. He coordinated the cataloging of the Diptera of the Oriental Region in the 1970s, the first and only comprehensive catalog from that region. He helped start the Hawaiian *Drosophila* project in 1963 which, with the help of numerous collaborators, increased the systematic and genetic knowledge of and stimulated world interest in a group of flies that exhibits one of the most explosive speciation and adaptive radiations of any animal on Earth—the genus *Drosophila* having upwards of 800 species known only from a tiny group of volcanic islands in the middle of the Pacific. In his almost 70 years of work on flies, he described 1,867 species in 34 different families of Diptera.

But his work in systematics was just a part of what Elmo did in the field of entomology and dipterology and is what was most publicized. What is not as well known were the workings — much like the Wizard of Oz — "behind the curtain" in his role as a professor at the University of Hawaii. In that capacity, he assisted numerous students, many from low-income backgrounds from Third World countries throughout the Pacific Rim area, in their education and their careers. Additionally, he was the answer-man for numerous public inquiries on "bugs" that came to the University. Some of these inquiries from housewives, farmers, nursery workers, and children, often led to unique discoveries of native and introduced invertebrates that otherwise might have gone unnoticed for many years.

Childhood and Schooling

Elmo (born Dilbert Elmo Hardy but preferred to keep the first name as an initial) was born in Lehi, Utah, the 3rd son of Horace Perham Hardy and Mary Ann Ivy (née Allred) Hardy. He had 3 brothers and 2 sisters. Home in Lehi was a small redbrick house near the center of town with two bedrooms, a kitchen, a living room, and a closed-in back porch, which was where they had their Saturday baths. The toilet was a privy in the backyard. His father owned the local candy store a few blocks away from home and Elmo had the run of the store, being allowed to eat as much chocolate and ice cream as he wanted. So much so that when he had his tonsils taken out at age 6, the doctor gave him — as doctors did with all kids getting their tonsils out — the traditional promise of having all the ice cream he could eat after the surgery. Although this was usually a dream-come-true for most kids, Elmo just sighed, "Big deal, I can get that all the time!"

Life at home was simple (no radio or telephones for diversions) and chores around the house helped Elmo learn about zoology at an early age. They kept cats as pets, and had chickens and goats. Whenever it was time to cook a chicken for a Sunday dinner, Elmo was asked to take care of the

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[1] Contribution No. 2003-018 to the Hawaii Biological Survey.

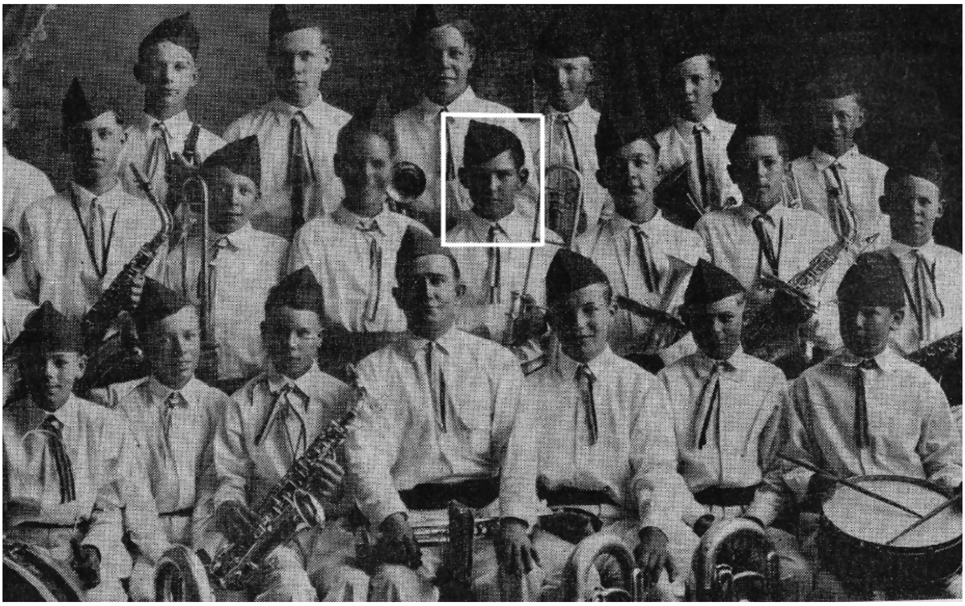

Figure 1. 1930 newspaper photo of the Miller's Boy's Band in Utah. Elmo is indicated by the square.

preparations for his mother including lopping off heads and plucking feathers. At age 10 he became interested in exploring the anatomy of the chicken before handing it off to his mother for cooking. Further interest in biology was stimulated by outdoor adventures with Elmo's Uncle, Charles Nostrom. Outings into the mountains west of Lehi would include gathering pine nuts and learning about bears, coyotes, foxes, beavers, etc.

The family was always interested in music and all Elmo's siblings played instruments. His sister Marjorie played the piano, his brother Horace played saxophone and clarinet, his brother Ken played clarinet, another sister Edith played the piano and trombone, his brother DeMour played trumpet, and Elmo played the trombone (Fig. 1). Elmo started playing at age 11 and played continuously until 1944, when a fall that damaged his teeth caused him to not be able to pucker up to the trombone mouthpiece any longer and he had to give it up. Elmo was an extremely talented trombone player and played in parades and bands with adults while still a child and even played in an Army band while stationed in India during World War II.

The family moved from Lehi to Tacoma, Washington when Elmo was 11 after his father quit the confectioner business and became a regional salesman for Utah Woolen Mills. Moving from a small provincial town to the "big city" was quite a shock for Elmo. This was really the first time he learned first-hand that there were people of different nationalities in the world and not everyone went to the LDS church. But it was there in Tacoma that he was taught biology by a teacher who was probably the one person responsible for pointing him in the direction of biology. She taught her students about the plants and animals of the area by bringing specimens into class and taking the class out to parks and Puget Sound and showing the students how and what to collect. She would explain how each plant or animal fit into the environment and further encouraged the students to read interesting books on natural history. An avid reader all his life, Elmo became fascinated by "*Waterton's Wanderings*", a multi-volume set of adventurous accounts of encounters with all sorts of animals from the Amazon Basin and the Orinoco in South America. Soon, Elmo was going out and collecting everything he could find, studying them, and taking them home. In no time his room was full of seashells, antlers, starfish, sand dollars, and other things that he could find near home.

After only a year in Tacoma, the family moved back to Utah after a relative died in an auto accident, but Elmo and his two brothers stayed in Tacoma a few more weeks to finish the school year. After school, his two older brothers went south to California by "riding the rails" and hoped to find work there, so Elmo was placed alone on the train back to Utah. It made quite a sight with a small 12-year old boy struggling with a large suitcase full of clothes, a trombone case, and 6-foot long moose antlers as he boarded the train back to Lehi.

A year after arriving back, the family moved a few miles south to Spanish Fork, Utah, where his father opened a lunch stand. It was at this time that Elmo became involved in taxidermy; it was a chapter in *Waterton's Wanderings* that also inspired this new adventure in Elmo's life. Elmo experimented with any animal he could get his hands on: birds of all kinds, squirrels, marmots, and deer and elk heads. One time his fervor got the best of him. He was busy preparing to stuff an owl, but apparently, the owl wasn't quite as dead as he thought and dug its claws into Elmo's chest. His sister Edith had to pry the owl off of a very surprised Elmo. Undaunted, Elmo continued to learn taxidermy through continued practice on several different animals. He became so proficient and well-known in the town as a taxidermist, that the mayor of Spanish Fork paid him to mount an elk head for his drug store, World Drug. It remained there for the next 60 years and still may be on the wall today.

Although no biology courses were taught in Spanish Fork, the fire had already been lit in Elmo and he was too busy collecting insects and other animals to notice. He used to arrange and classify his insect collections every afternoon at his father's lunch stand. Stacks of cigar boxes full of insects around the lunch stand soon caused the townspeople to talk and it was not long after that Elmo became known in the community as "that crazy Hardy kid". Insects were not the only things he collected. By the time his older brother Horace moved out of his room, Elmo quickly turned it into a small "museum" filled with gallon after gallon of pickled snakes, reptiles, skins of all sorts of animals, rocks, mounted birds — anything he could drag in. A recent road-kill coyote was brought in late one night after tying it to the hood of the car and Elmo was anxious to find out what was in its stomach. The next morning he awoke to the whole house full of fleas from the coyote, but was further fascinated to find out that the stomach was full of grasshoppers.

University Years

After graduating from high school in 1931, Elmo played in bands in Montana and worked in a sugar factory there for a couple of years before entering Brigham Young University (BYU) in 1933. Vasco Tanner was then chairman of the entomology department and put him to work in the collection for his tuition. Elmo majored in entomology while minoring in German. Entomology was quite easy for Elmo since he had virtually memorized Comstock's "Introduction to Entomology" while still in high school. By the time he enrolled at BYU as a freshman, he was tutoring juniors and seniors in entomology. He graduated from BYU in 1937, but not before he married his first wife, Agnes Dale Thomas on 6 September 1935, her 20th birthday. While at BYU, Elmo published his first paper, on a new species of bibionid (*Bibio melanopilosus*) in 1936. He published one more paper while at BYU, in 1937.

After graduating, Elmo immediately got a job at Utah State University working on tomato insects. He enrolled in graduate school there and was awarded a research assistantship. But his trombone talent also helped pay the bills and Elmo continued to play in various bands while attending school. After one year at Utah State, he was awarded a teaching assistantship at the University of Kansas (KU). He and Agnes quickly loaded up their Model A Ford with their few belongings and headed across country to Lawrence, Kansas.

In the entomology department at KU (Fig. 2), Elmo majored in taxonomy and systematics and minored in medical and veterinary entomology, specializing in parasitology. The PhD program at KU was a busy one for Elmo and he had to give up his trombone playing during that time. He received $50 per month for his teaching assistantship and the time he needed for teaching and prepa-

Figure 2. 1940 entomology class at the University of Kansas. Elmo is standing at the far right. Others identified in the photo include: Back row: Charles Shepard (3rd from left), Laurence Woodruff (8th from left), Reece Sailer (9th from left). Front row: Raymond H. Beamer (4th from left), Kathleen Doering (5th from left), Herbert B. Hungerford, Department Chair (6th from left), and Bob Guntert (9th from left).

ration unfortunately interfered with his required coursework. Some of the courses he needed to take were scheduled at the same time he needed to assist in the labs. But he and Agnes devised a solution. He made a deal with the professors teaching those courses that Agnes could sit in and take notes for Elmo. She did such a great job that Elmo ended up getting straight "A"s in all of his classes.

The years at KU were very productive for Elmo. He wrote 19 scientific papers including 2 large monographs (one of those two monographs was his Ph.D. thesis on Pipunculidae, which came to about 230 printed pages). The original thesis Elmo presented to the department (ca. 1,000 pages) was the largest thesis ever submitted to KU at that time. As always, Agnes did all of the typing. When he finally received his degree, the department chairman joked "We should be giving this degree to Agnes, since she did all the work."

After receiving his PhD, Elmo took a short job in the Kansas State Entomologist's Office as nursery inspector, then took a position with the U.S. Department of Agriculture for a few months as a field supervisor for the Chinch Bug Survey in the central states and the Pear *Psylla* Survey in the Pacific Northwest, the latter working mainly out of Spokane and Yakima, Washington. The government job was not to Elmo's liking— "too much bureaucracy"— so he quit and went back to working at the Kansas State Entomologist's office and as a post-doc at KU doing research on flies until he went into the Army in May 1942.

World War II

After being told the military needed medical entomologists and he could get a commission, Elmo entered the Army and was given a direct commission as a 1st lieutenant in the Sanitary Corps. He was called to active duty on 11 May 1942 and assigned to O'Reilly General Hospital in Springfield, Missouri. During his initial training he shared a lab with some future famous entomologists including Harry Hoogstraal, Stanley J. Carpenter, Frank N. Young, Louis Roth, and others (Fig. 3). After a month at Springfield, he received his first "permanent" assignment at Morrison Field, West Palm Beach, Florida, which was a staging area for the Air Force and medics being sent to Africa, the Middle East, India, Burma, and China. Most at Morrison had never seen a case of malaria or a tropical disease, so the Army decided to set up a training school and Elmo was selected to teach Medical Entomology. After three months of tropical disease training, they graduated their first class; and the Army sent them all to ... Alaska.

Figure 3. Medical entomologists in training at O'Reilly General Hospital in Springfield, Missouri, 1942. Some of those identified in the photo include Elmo Hardy (0), Harry Hoogstraal (12), Woodrow W. Middlekauf (7), Louis Roth (11), Frank N. Young, Jr. (8), and Stanley J. Carpenter (2).

After being promoted to captain a few months earlier, in March 1943 Elmo got his orders to go to Assam. He was to be in charge of Medical Entomology for the Air Force in the CBI (China-Burma-India) Theater. Flying to Chabua in Assam by Army transport was a two-week adventure that took him to Georgetown, British Guiana [now Guyana]; Recife, Brazil; Asunción Island, Atlantic Ocean; Accra, Ghana; Dakar, Senegal; Lagos, Nigeria; Kano, Nigeria; Madugeri, Chad (where he and his fellow travelers went exploring in the desert and were set upon by about a dozen wild looking natives on horseback galloping toward them with knives raised — it turned out that all they wanted to do was sell them souvenirs!); Khartoum, Sudan; Massaua, Eritrea; Aden, Yemen; Salala, Saudi Arabia; Karachi, Pakistan; Delhi, Patna, Jorhat, and finally Chabua, Assam, India (the last 1,000 miles flying at tree-top level to avoid cruising Japanese zeroes). The Air Force headquarters were in Delhi, a relatively safe haven from the war, and it was from there that Elmo's commanding officer, a man who craved excitement and action, decided to post the Sanitary Corps toward the front lines in Chabua, Assam, a mere 30–40 miles from the front.

While in Assam, Elmo was promoted to major and put in charge of control and prevention of insect diseases for all of CBI. He was in charge of approximately 250–300 personnel. After losing his malariologist colleague to a medical discharge, Elmo added malariologist to his duties. He spent the equivalent of several months studying whenever he could at the School of Tropical Medicine in Calcutta and became a frequent visitor there making many friends. His experience with tropical diseases and medical entomology in general helped him greatly in his eventual teaching duties at the University of Hawaii after the war; they were subjects he always was fond of teaching.

Chabua was the central supply for all the troops in the CBI and 30–40 flights left Chabua each day supplying the troops in the field as well as sending out rescue parties in search of downed fly-

Figure 4. Major D. Elmo Hardy with "pet" python in Chabua, Assam, India.

ers. Soon after it became apparent that loss of the flight crews out of Chabua was heavy in that jungle terrain, a survival course was given to all personnel. The Sanitary Corps made sure that all parachute kits contained leech and mosquito repellent, nets, etc. Elmo had a pet gibbon and they soon learned from the gibbon which plants and insects were safe to eat for survival.

In addition to the gibbon, Elmo's crew also collected snakes while in Assam, most eventually to be sent back to the National Zoo in Washington, D.C. One of his crew, Wesley Dickinson, was a zoo person and had extensive experience working with live snakes and taming them. They erected a building especially to house all the snakes that they collected and tamed. They had king cobras, vipers, pythons, rat snakes, etc. Elmo eventually sent back 800 pounds of live snakes to the National Zoo (Fig. 4).

All was not fun and games, however. His charge was to control and prevent diseases in Assam and eventually also in Calcutta, the new headquarters for the Air Force. Calcutta was the biggest challenge he faced during the war, but through his efforts, his crew was able to significantly reduce the incidence of disease and resulting deaths. In February 1944, his unit was awarded a Presidential Unit Citation and a combat ribbon and Elmo himself was awarded a Bronze Star for his efforts in disease control and prevention over India, Burma, and China.

University of Hawaii

Soon after the war, Elmo and his family moved to Ames, Iowa, where Elmo had accepted a job as Assistant Professor of Entomology at Iowa State University. He was hired by Carl Drake to teach medical and veterinary entomology and do research in Diptera taxonomy. After he arrived for work, he found out that their quarantine entomologist had left due to old age and they were looking for a replacement. Elmo was asked to step in temporarily as Assistant State Entomologist to conduct nursery inspections. He did so for the next three years with Wally Mitchell as his assistant. Wally and Elmo were soon best friends, a relationship that continued into their shared years teaching at the University of Hawaii.

In June 1948, Elmo was offered jobs at the University of Florida and the University of Hawaii. Extremely anxious to get away from the cold winters of Iowa, Elmo and his family decided to go to Hawai‘i and treat it as a "short vacation", never thinking that it would be a permanent situation.

In October 1948, Elmo, Agnes, and their children (the youngest just born 6 weeks earlier) arrived in Honolulu (Fig. 5). Elmo was hired as an Assistant Professor and was promoted to full professor a few years later. Shortly after settling in Hawai‘i, Elmo began to travel to all the islands to collect and amass as much information and specimens as possible for the Diptera volumes of the *Insects of Hawaii* series. When Elmo arrived in Hawai‘i, only 197 species of flies were recorded. After publication of 5 volumes of the *Insects of Hawaii* devoted to Diptera (1960–1981), there were 1,209 species known.

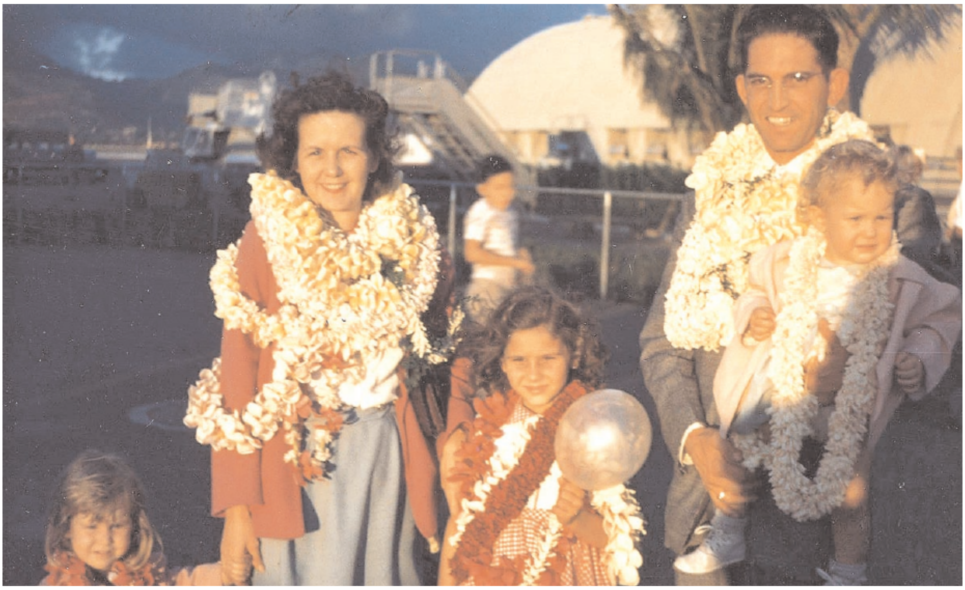

Figure 5. The Hardy family arrives at Honolulu International Airport in October 1948. Left to right: Joan, Agnes, Patricia, Elmo, and Cheryl [Dee (born 6 weeks earlier) not pictured].

Teaching and research occupied Elmo's working hours for the next few years and the Hardy home was open to all the students that cared to come by. The Hardys were wonderful hosts and took special pleasure in making their home available to everyone, especially the international students with whom it was a joy to see interact with other students from all over the world. There were no language, economic, or color barriers in the Hardy home and they made lifelong friends with all of the students.

In 1954, Elmo went on his first sabbatical, to study types of Hawaiian Diptera in European museums for his *Insects of Hawaii* series. The first 3 months were spent in London at the British Museum (Natural History) [now The Natural History Museum]. It was there that Elmo developed a quick way to describe flies. He used a Dictaphone rather than write descriptions long-hand (Elmo did not type). Agnes later transcribed the recordings and Elmo would edit the typed versions. Elmo continued to use this method throughout the rest of his career. He claimed he was able to get one year's worth of work done in London in just 3 months in this fashion. After London, Elmo's sabbatical took him to Ghent, Brussels, Amsterdam, Leiden, Paris, Rome, Padua, Florence, Milan, Berlin, Stuttgart, and Vienna.

Succeeding years saw Elmo traveling to Australia, New Guinea and Indonesia for fieldwork; to Europe on an NSF-sponsored sabbatical in Vienna in 1961 and another to Europe, India, Southeast Asia, and the Philippines in 1968–1969; and to congresses and other meetings in Beijing, Bogor, Bratislava, Brisbane, Budapest, Kuala Lumpur, Kyoto, London, etc.

The Hawaiian *Drosophila* Project

In 1963 Elmo embarked on a project that was to be one of the most prodigious and important for decades to come. After traveling throughout the Hawaiian Islands to survey and assess the Hawaiian Diptera fauna, it became apparent to Elmo that Hawai'i was exceptionally fertile ground for evolutionary studies and that one group of flies in particular had taken the opportunity to evolve into many species to the extreme. For 50 years, species in the family Drosophilidae (especially *Drosophila* *melanogaster*) had been among the premier animals used the world over for genetics research because they have giant chromosomes that are easily studied and they are easily reared in laboratories. In Hawai‘i, the species of the genus *Drosophila* have not only speciated tremendously (almost 400 endemic species — ca. one-third of the world's fauna), but include a significant number of species in which gigantism has occurred. The explosive evolution of these flies intrigued Elmo and he started giving seminars wherever he went extolling the virtues of Hawai‘i as a "living laboratory of evolution". When Elmo gave a speech at the University of Texas, it did not take long for geneticist Wilson Stone to be convinced and he quickly worked with Elmo in writing a grant proposal to conduct work on what would become known as the Hawaiian *Drosophila* Project. The National institutes of Health intitally funded the program for about 5 years before the National Science foundation helped with funding. The founding participants in the project included such luminaries as Hampton L. Carson, Marshall Wheeler, Frances E. Clayton, William B. Heed, Herman T. Speith, Harrison D. Stalker, and H. Lynn Throckmorton. Research began in June 1963 and further collaborators such as Michael Kambysellis, Elysse Craddock, Theodosius Dobzhansky, Francisca C. do Val, Jong Sik Yoon, Alan Templeton, and others took up the mantra.

In the succeeding decades, hundreds of new species were described and countless scientific papers published the results of research including behavior, genetics, ecology, larval biology, as well as the systematics of *Drosophila* and its closely related genera. Collaborators eventually counted into the dozens, visiting scientists numbered into the hundreds worldwide, and numerous graduate students became intimately involved and in some cases contributed seminal insights into the biology and evolution of these flies.

The project was one of the most successful biology projects ever funded in Hawai‘i and continues to this day under the leadership of Ken Kaneshiro, who started with the Project in October 1963 as second year undergraduate student. Although it has increased our knowledge of the biology, systematics, and evolution of Hawaiian drosophilids, the Project will be forever known as the one that put Hawaiian evolutionary biology on the map and let the world know how unique and exciting the Hawaiian biota is. So much so that one preeminent biologist once said if Darwin had visited Hawai‘i instead of the Galápagos, all the textbooks would be referring to examples of Hawaiian species radiations and not the Galápagos.

Other Diptera Research

Outside of Elmo's pioneering work with Hawaiian *Drosophila*, he was also a world's authority in 3 other fly families: Tephritidae, Pipunculidae, and Bibionidae. He contributed the results of his research on all 3 families throughout his career, but spent the last 20 years working almost exclusively on Tephritidae, including collaborative work with Dick Drew and Richard Foote.

Elmo's interest in Tephritidae was sparked during his first trip to London to study the types of Hawaiian Diptera. He laid the groundwork then for future studies by taking the opportunity to examine and try to make sense of the tephritid types of Francis Walker which, up till then, had not been systematically researched. It soon became apparent that one trip to London was not going to solve all the problems in tephritid taxonomy, so Elmo embarked on a lifelong task of revising many of the taxa in the family. In his 67 years of Diptera research, he published 48 papers on the systematics of Tephritidae and described 465 new species and 78 new genera (see Evenhuis & Thompson, this issue, for more details on the taxa described).

Elmo's early experience in economic entomology in Utah, Iowa, and the Pacific Northwest and his work on Tephritidae after his arrival in Hawai‘i led to him traveling to Indonesia and Malaysia to attend conferences on Tephritidae and agricultural entomology. These meetings were not only beneficial in disseminating information on fruit fly taxonomy and agricultural impacts, but also led to him making lifelong friends and colleagues from these and neighboring countries. In addition, many of Elmo's foreign graduate students at the University of Hawaii ended up going back to their native countries and working in agricultural entomology and requested visits by Elmo to give lectures or help with research in those countries. He always obliged.

Table 1. Chronology of Events in the Life of D. Elmo Hardy

3 September 1914	Born, Lehi, Utah
June 1931	Graduates from High School
September 1933	Enters Brigham Young University, Provo
6 September 1935	Marries Agnes Dale Thomas
July 1936	First paper, first new species (*Bibio melanopilosus*)
June 1937	Graduates from BYU with B.A. degree
September 1937	Enters Utah State University, Logan
June 1938	Graduates Utah State University with an M.A. degree
September 1938	Enters Kansas University, Lawrence
June 1941	Graduates from Kansas University with PhD
11 May 1942	Enters US Army as 1st Lieutenant
22 March 1943	Leaves for Assam
5 October 1944	Returns home from India
December 1944	Stationed at Harlingen Air Force Base, Texas
October 1945	Released from Army; takes job at Iowa State University as Assistant Professor
June 1948	Offered job at University of Hawaii
June–July 1948	Visits USNM to do Diptera research before going to Hawai‘i
October 1948	Arrives Hawai‘i, Assistant Professor, University of Hawaii
April–November 1954	First Sabbatical to European museums
June–September 1957	Bishop Museum New Guinea Expedition
1958–1968	Chair of UH Department of Entomology
1960–1961	Second Sabbatical to European museums
1960–1981	*Insects of Hawaii* published (5 volumes)
June 1963	Starts Hawaii *Drosophila* Project
1968–1969	Sabbatical to European, Indian, SE Asian, and Philippines museums
1973–1977	*Catalog of Oriental Diptera* published (3 volumes)
January–September 1975	Sabbatical to Indonesia
December 1976	Entomology Society of America National Award for Outstanding Research
July–October 1979	Research trip to Indonesia/Australia
December 1980	Retires from University of Hawaii
June 1981	University of Hawaii Regent’s Medal of Excellence in Research
29 October 1985	Agnes passes away
6 May 1988	Marries Ilse Hildegard Erdmann Riehl
February 1993	Hawaiian Entomological Society Award for Lifetime Excellence
24 June 1998	University of Hawaii Regent’s Medal of Distinction
17 October 2002	Passed away, Honolulu, Hawai‘i

Work on Pipunculidae began in 1939 with 3 papers on Nearctic species, then got serious with his doctoral dissertation, and continued for 50 years. In that time, Elmo described 346 new species and subspecies in the family (see Skevington & De Meyer, this issue, for more details on Elmo’s impact on Pipunculidae systematics). Bibionidae was Elmo’s first love in Diptera and resulted in his first 2 papers describing new species. And speaking of “love”, Elmo is responsible for describing and naming the now-famous “love bug” of the southern United States (*Plecia nearctica*) — so named because swarms of them are often found *in copula*. Elmo described 305 new species and 3 new genera in Bibionidae. During his years of research on this family, Elmo amassed important synoptic collections of the world’s genera and species of Pipunculidae and Bibionidae. In 1992, both of these collections were donated to the Bishop Museum, where they are currently preserved for the benefit of researchers worldwide.

Figure 6. Elmo and Ilse at the 1998 UH Regent's Medal ceremony.

Later Years

The 1980s were bittersweet for Elmo. In those 10 years, he retired from teaching, suffered the loss of Agnes to pancreatic cancer, and re-married in 1988.

After serving the University as professor and graduate advisor for 32 years and chairing its department from 1958 to 1968, Elmo finally retired from the University of Hawaii in December 1980. His Emeritus years were productive, but the luxury of space and time soon came to a crashing halt. In just a few short years after his retirement, his working space was reduced to a small 6 × 9 ft. office that had a desk with his dissecting scope on it and a few bookshelves (the laboratory was taken over by graduate students studying biological control under another professor). He eventually was forced to leave even his small office and was given a small space in the university's insect museum. This move was extremely depressing for Elmo, who had a huge library in the laboratory that needed to be dismantled because there was no room to move it anywhere else (space being precious in the Entomology Department). Elmo had acquired a great many volumes of old books on Diptera taxonomy during his decades of research. He was especially fond of the many books he acquired from bookstores in India during World War II including a full set of the *Fauna of British India*. He also had a great many journals including some full runs that were otherwise not held by any library in Hawai'i. After some deliberation, he ended up splitting a donation between the University library and the Bishop Museum.

Suffering through Agnes's cancer and her eventual death was the biggest blow for Elmo. Family was extremely important to him and his whole life and even career revolved around the undying support of Agnes and her assistance in his many projects. She joined him on his sabbaticals to Europe and helped with his manuscript preparation. She always swam next to him on their morning ocean swims. Additionally, she, as well as their children, often joined him on his many collecting trips throughout the Hawaiian Islands. Her strength as a homemaker, being a loving mother to their children, and lifelong companion to Elmo, as well as her cheerfulness at being hostess to countless visitors would be sorely missed. His children were by now grown and had moved away. Elmo was alone for the first time in his life. His work suffered a downturn in productivity and the primary traveling that he did was to visit his children on the mainland and Agnes's grave in Spanish Fork, Utah.

But his loneliness was to be short lived. A family friend, Ilse Hildegard Erdmann Riehl, kept in close contact with Elmo soon after the death of Agnes. She and Agnes had worked together 20 years earlier. The two became very close friends and always stayed in touch. It was only natural then that Elmo turned to Ilse for companionship. The two got along very well and were married on 6 May 1988 in a ceremony in Virginia attended by many of Elmo's Diptera colleagues who worked in nearby Washington, D.C.

His marriage to Ilse renewed his energy and his work on Diptera soon got back on track again with gusto. With Agnes gone, graduate students or departmental secretarial staff did much of his typing chores. Every week, sometimes daily, he and Ilse did their morning ocean swim at Ala Moana Beach Park, then it was on to the University to check mail and finish up sometimes as many as a half a dozen different papers that were in various stages of completion.

This routine continued for a number of years. Then he had a major setback. Upon his return from the International Congress of Entomology in Beijing in 1992, Elmo suffered a stroke. The stroke paralyzed him on one side and severely restricted his speech. After swimming every day in the ocean as his rehabilitation, he improved quickly but was slow to get back into the normal routine. He always showed up for the quarterly Hawaiian Entomological Society meetings and his progress in walking and speaking became evident at each successive meeting. After a few years Elmo was pretty much back to normal. His routine may have been a little slower, but was always the same: swim in the mornings and then off to the University to check mail and work on manuscripts.

The year 1998 was to be a special one for Elmo. Through the coordination and efforts of a number of colleagues, Elmo and Elwood C. Zimmerman ("Zimmie") received the University of Hawaii's Board of Regent's Medal of Distinction in honor of their contributions to the internationally renowned *Insects of Hawaii*, which was marking its 50th anniversary since Zimmie founded the series in 1948. A lavish ceremony (Fig. 6) in concert with a special symposium with paper presentations by numerous colleagues in their honor was followed by a special reception at College Hill, the historic Hawaiian home of the President of the University of Hawaii. Elmo was humbled by all the fuss and proceedings and refused to make a speech, saying he "had given up public speaking years ago". However, the rare image of Elmo and Zimmie together for the first time is one that no one who was there that evening will ever forget.

Elmo was always humble yet had a certain strength of character and perseverance that got him through most of the difficult times in his life. However, that strength that he had in overcoming his personal losses and stroke were not enough to survive a broken hip that occurred after falling at home in September 2002. After seeming to be making a comeback in the hospital, he caught pneumonia and took a turn for the worst. He tried to battle it, but soon gave way to the inevitable and passed away on 17 October 2002.

Epilogue

With Elmo gone, we have lost much more than a well-respected Diptera systematist and teacher. We have lost a link to a previous generation of research that was more generalized and one that crossed many disciplines in order to be able to acquire and understand our environment and the way things work in biology. We have also lost a good friend. Probably more important to Elmo than his work was his family. And his "family" included more than his own kin. They were all the past and present students who studied under or came into contact with Elmo. They were his colleagues. They were his many friends. He was always eager to assist and took great pleasure and pride in seeing the successes of those whom he met, taught, and collaborated with over the years. We will miss him.

Acknowledgments

Much of this biography was gleaned from Elmo's unpublished autobiography, a voluminous work of almost 600 typewritten pages that was created for his children and grandchildren so that they would know what he did in his life. I am deeply appreciative to Ilse for allowing me to borrow this "family treasure" for this biographical piece and to reproduce the photographs of Elmo used in this biography. Steven Montgomery generously supplied the photograph of Elmo and Ilse at the University of Hawaii Board of Regent's Medal of Distinction ceremony. Charles D. Michener and George Byers kindly assisted with names of persons in the 1940 Kansas University entomology photo. Ken Kaneshiro, Frank Howarth, Scott Fitzgerald, Marc DeMeyer, Jeff Skevington, Chris Thompson. and Ilse Hardy kindly reviewed various drafts of the manuscript and their comments have helped improve it.

D. Elmo Hardy Memorial Volume. Contributions to the Systematics and Evolution of Diptera. Edited by N.L. Evenhuis & K.Y. Kaneshiro.
Bishop Museum Bulletin in Entomology 12: 13–25 (2004).

Pipunculidae Research by Elmo Hardy: Another Founding Event on the Hawaiian Islands

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Abstract

For 50 years, D. Elmo Hardy studied the dipteran family Pipunculidae. During that period he produced numerous articles, covering all taxonomic groups within the family and nearly all zoogeographical regions. His contribution to the knowledge of the group has been tremendous and pivotal for all future work. This article gives an overview of the taxonomic knowledge prior to Hardy's work, his contribution from 1939 until 1989, and the impact of his study on the contemporary research of the last decades.

Introduction

Pipunculidae or big-headed flies are distinctive, but inconspicuous, relatives of the Syrphidae (hover flies or flower flies). Over 1,300 species have been described worldwide and it is estimated that well over 2,000 species exist. They can be differentiated from syrphids by the large compound eyes that occupy most of their hemispherical head, the distinctive wing venation (no *vena spuria*, cell r4+5), the chitinized postspiracular plate found in the larvae, and their unique life history. During their larval stage they are known as endoparasitoids of several families of Auchenorrhyncha (Homoptera). It is because of this parasitoid lifestyle that Elmo Hardy started studying the representatives of this family. His first endeavors focused on Nearctic fauna but later covered material from all zoogeographical regions. For 50 years (1939 to 1989) Hardy studied the group, although he published most of his articles on this family between 1939 and 1972. Later, his interests turned completely towards other dipteran groups although he did produce some occasional papers after 1972. His main contribution was on descriptive taxonomy (alpha taxonomy), and cataloging particular faunas.

Early Work on Pipunculidae

The first pipunculid species were described at the turn of the eighteenth century (Bosc, 1792; Latreille, 1802; Meigen, 1803). Throughout the early nineteenth century, descriptions of new species were sparse and occasional (Fig. 1) and were mainly based on Palaearctic material. Descriptions of "exotic" (i.e., non European) Pipunculidae were rare (e.g., Wiedemann, 1830) and usually formed part of general works dealing with several dipteran families. By the end of 1897 only 85 species were described, with 74% originating from Europe. Only one paper focusing solely on this family was published before 1897 (Walker, 1834).

At the turn of the 19th Century, some more detailed studies appeared, in particular by Theodor Becker, a German entomologist. In his two major papers (Becker, 1897, 1900) he described 38 partly non-European species and produced the first major classification, splitting the genus *Pipunculus* into different species groups. In the Nearctic region, E.T. Cresson published a review of the North American species, describing several new species (Cresson, 1911). His monograph was the result of a two-year study and included notes and comments made by Nathan Banks. Material from other geo-

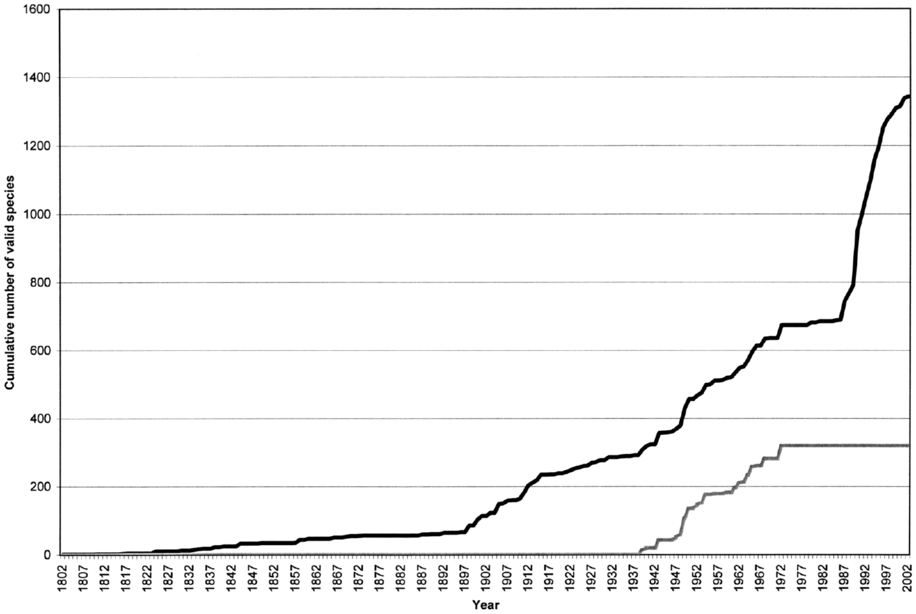

Figure 1. Cumulative curve of Pipunculidae species described over time (top black line: all authors; bottom gray line: species described by D.E. Hardy).

graphical regions, like Asia, soon became available to researchers and resulted in publications of the pipunculid faunas of those areas. Noteworthy in this respect is Kertész's work (1903, 1907, 1912).

During the 1920s and early 1930s a lull appeared in descriptive work on Pipunculidae (Fig. 1). The major researchers active in that period were J. Collin (England) and C.H. Curran (North America). Collin produced revisions of the British representatives of taxonomic entities within the family, in particular the genus *Pipunculus*, like the *sylvatica* group (now the genus *Tomosvaryella*) (Collin, 1920) and the *rufipes* group (now the genus *Dorylomorpha*) (Collin, 1937). Curran described several American and non-American species (Curran, 1927, 1928a, 1928b, 1929, 1934a, 1934b, Curran *et al.*, 1936). Nevertheless, the number of described species remained low. By 1938, 292 pipunculid species were described worldwide (Table 1). Palaearctic and Nearctic species comprised 125 (43%) of these. Of the genera recognized today, most representatives were from the genera *Eudorylas* and *Tomosvaryella* (Table 2).

Contribution by D. Elmo Hardy

Hardy started working on Pipunculidae in the late 1930s. His interest in this group started as a research fellow at the Utah Agricultural Experiment Station in Logan, Utah where he worked under George Franklin Knowlton. One of his interests was the sugar-beet leafhopper [*Eutettix tenellus* (Baker)]. Parasitoids of this pest species were studied in order to find a biological control agent that could regulate the populations (Hardy & Knowlton, 1939a). Pipunculid species were found to be of considerable importance in this respect (Knowlton, 1937). During their investigations, Hardy and Knowlton realized that several species, especially in the western states of the USA were unknown to science. The first articles on Pipunculidae by Hardy dealt with these parasitoids and two were written with Knowlton as co-author (Hardy, 1939; Hardy & Knowlton, 1939a, b). Hardy's further exploration of Nearctic Pipunculidae promoted the importance of male genitalic characters for an unam-

Table 1. Comparison of faunal knowledge over time by region (number of valid species)

Region	**1938**	**1972**	**2002**	**Hardy only**	**% by Hardy**
Exclusively Nearctic	36	85	120	46	38.3
Exclusively Neotropical	33	103	239	70	29.3
New World	9	11	14	1	7.1
Exclusively Palaearctic	88	142	495	4	0.8
Holarctic	4	8	9	2	22.2
New World/Holarctic	2	3	3	1	33.3
Palaearctic/Oriental/Australasian/ Oceanian	4	6	6	1	16.7
Palaearctic/Oriental	17	22	22	3	13.6
Exclusively Afrotropical	17	125	149	105	70.5
Exclusively Oriental	34	81	148	47	31.8
Oriental/Australasian/Oceanian	5	9	9	4	44.4
Exclusively Australasian/Oceanian	35	71	119	36	30.3
Cosmopolitan	1	1	1	0	0
Holarctic/Oriental	3	3	3	0	0
Palaearctic/Afrotropical	1	1	2	0	0
Palaearctic/Australasian/Oceanian	0	0	1	0	0
Palaearctic/Afrotropical/Oriental	1	1	1	0	0
Palaearctic/ Afrotropical/Oriental/ Australasian/Oceanian	1	1	1	0	0
Note: No data available in database for region: (nomen dubium: *Tomosvaryella unguiculatus* Loew 1860).	1	1	1	0	0
Totals:	**292**	**674**	**1343**	**320**	**23.8**

biguous identification of pipunculid species. This was probably partly due to his contact with the Hungarian entomologist Martin Aczél who, at that time, was one of the main European researchers working on this family (Hardy, 1940). Although Aczél did some descriptive work, his main interests were on the phylogeny of the group and reviewing previous research (on elements such as host-parasitoid records, higher classification, fossil record, and phylogenetic reconstruction). Aczél left Hungary for Argentina after the World War II for political reasons. His subsequent work on Pipunculidae became limited and stopped after 1948. Hardy was in contact with Aczél, but apparently did not collaborate or produce joint papers with him.

Elmo Hardy had by the late 1930s moved to the Department of Entomology at the University of Kansas and had embarked on a monographic study of the Nearctic representatives of the Pipunculidae. This revision formed part of his thesis in partial fulfillment of the requirements of a Ph.D. degree and was published in the *University of Kansas Science Bulletin* (Hardy, 1943). The monograph is 231 pages, and provides an introduction to the group with elements on their taxonomy, morphology, biology, and collecting methodology. It continues with a brief description of all world genera, and a taxonomic revision of all Nearctic species, comprising 117 species, subspecies and varieties (including 27 new ones). A large part of the study was based upon recently collected material, with a strong emphasis on the western U.S.; partly by the Beamer expeditions (Hungerford, 1958) and partly by Hardy himself. Together, Beamer and Hardy had the most productive collecting of southwestern pipunculids ever documented during their 1940 trip to Arizona. For example, they collected dozens of pipunculids including over 60 specimens of 7 species of *Pipunculus* on 4 July 1940 in the Chiricahua Mountains (Skevington & Marshall, 1998). Although Hardy mentioned the paucity of information on host relationships, he apparently never reared pipunculids; however, he did

Table 2. Comparison of faunal knowledge over time by genus (number of valid species)

Genus	1938	1972	2002	Hardy only	% by Hardy
Allomethus	0	3	5	2	40.0
Amazunculus	0	1	3	1	33.3
Basileunculus	2	2	3	0	0.0
Cephalops	35	112	179	72	40.2
Cephalosphaera	10	25	52	14	26.9
Charalus	7	13	41	1	2.4
Claraeola	5	11	20	6	30.0
Claraeosphaera	0	0	1	0	0.0
Clistoabdominalis	10	11	34	1	2.9
Collinias	3	4	5	1	20.0
Dasydorylas	7	15	16	7	43.8
Dorylomorpha	18	30	83	9	10.8
Elmohardyia	5	17	51	12	23.5
Eudorylas	99	237	416	121	29.1
Jassidophaga	7	10	24	1	4.2
Microcephalops	6	23	31	16	51.6
Nephrocerus	5	5	14	0	0.0
Pipunculus	16	23	71	4	5.6
Protonephrocerus	1	1	1	0	0.0
Tomosvaryella	47	110	270	51	18.9
Verrallia	2	4	6	0	0.0
Incertae Sedis	7	17	17	1	5.9
Totals	**292**	**674**	**1343**	**320**	**23.8**

make numerous references to possible associations of leafhoppers found in the vicinity of the collecting sites.

After his period at the University of Kansas and as an officer and medical entomologist during World War II, he was appointed Assistant State Entomologist at Ames, Iowa and, by the end of the 1940s, moved to the University of Hawaii where he would stay until retirement. His dipterological interests would widen but throughout the following 3 decades (until 1972) Hardy would continue publishing on Pipunculidae. The first papers after the 1943 monograph dealt with nomenclatorial notes (Hardy, 1946) and further additions or elaborations on his findings regarding Nearctic Pipunculidae (Hardy, 1947, 1948a). He started dealing with the faunas of other zoogeographical regions as well. First, he studied exotic material in the Museum of Comparative Zoology, the American Museum of Natural History, the U.S. National Museum, Ohio State University, and the California Academy of Sciences (Hardy, 1948b, 1948c, 1949a). Much of this material was from the Neotropics and it seems to have been Hardy's plan to produce a monograph of the Neotropical Pipunculidae, probably comparable to his Nearctic work (Hardy, 1948c: 1; see also Hardy 1953a: 299). Although no such monograph was ever published, he did produce several articles on the Neotropical Pipunculidae over the next 17 years (Hardy, 1950b, 1954a,b, 1962a, 1963, 1965a,b). These articles dealt with collections that were put at Hardy's disposal, often of particular countries. Included was Aczél's collection made in Argentina, which could not be studied by Aczél himself due to his untimely death (Hardy, 1965a).

In 1949, he also produced a monograph on the Afrotropical pipunculid fauna (Hardy, 1949c), including the south Mediterranean region. However, the work was rendered obsolete soon after publication because of much new additional material that could only be studied after completion of the monograph. The new material was largely from the Democratic Republic of Congo. Several general expeditions were organized by Belgian researchers to the different National Parks that were newly erected in the then Belgian Congo and material of these expeditions was sorted and sent to specialists worldwide. Hardy published a number of papers, often dealing with both Pipunculidae and Bibionidae of the several different parks (Hardy, 1949b, 1950a, 1952a, 1959b, 1961) as well as other material from the former Belgian colonies present in the Royal Museum for Central Africa, Tervuren and the Royal Belgian Institute for Natural Sciences (Belgium) (Hardy, 1952b, 1952c, 1955). In addition, he studied collections made in South Africa (Hardy, 1959a, 1962a), Madagascar (Hardy, 1962b), Mauritius (Hardy, 1956a), and Tanzania (Hardy, 1960). All of these resulted in a thorough contribution to the knowledge of the pipunculid fauna of the African continent.

His move to Hawai'i also initiated the study of the Hawaiian fauna. As with many other elements of the Hawaiian fauna, the pipunculid diversity is the result of a single founder event with successive dispersal throughout the archipelago and high speciation rate (De Meyer, 1996). Some knowledge was available on the Hawaiian Pipunculidae prior to Hardy's study. Most of this was gathered by R.C.L. Perkins (1905, 1906), who worked for the Experiment Station of the Hawaiian Sugar Planters' Association, in connection with work on the parasites of homopteran pests. The first addition to Perkins' Hawaiian work was published by Hardy (1953b). Later, he revised his work on Hawaiian pipunculids (Hardy, 1964b) as part of the ongoing *Insects of Hawaii* series. Most of the new species described by him were based on material that he collected personally on the different islands of the archipelago. Probably in conjunction with this work, Hardy also studied some other collections housed in the Bishop Museum, Honolulu and published some papers on the fauna of the Micronesian islands (Hardy, 1956b) and Australian type material described by Perkins (Hardy, 1964a).

Studies of the Oriental fauna started somewhat later than for other regions. Again, parts of this research was based on collections put at the disposal of Hardy, like the material of the Danish Noona Dan Expedition to the southern Philippines and Bismarck Islands (Hardy, 1968), the Swedish Expedition to Burma (Hardy, 1972a), and the British Museum expedition to East Nepal (Hardy, 1966b). However, part of this research also based on material collected by Hardy himself in the Philippines. A paper reviewing data on pipunculids parasitic on rice leafhoppers in the Orient (Hardy, 1971) summarized the impact of big-headed flies on this economically important group of pests. A review of the Oriental fauna published in 1972 (Hardy, 1972b) largely marked the end of Hardy's active pipunculid research, although he did publish some occasional papers on the family like the chapter in the *Manual of Nearctic Diptera* (Hardy, 1987).

In addition to his taxonomic papers, Hardy also produced catalogs for all zoogeographical regions, except the Palaearctic region (Hardy, 1965c, 1966a, 1975, 1980, 1989).

Hardy was involved in 2 different nomenclatural disputes that were submitted to the International Commission on Zoological Nomenclature (Hardy, 1951a,b, 1958). The first dispute revolved around the use of Meigen 1800 names that had been out of circulation for over 100 years before being discovered and pressed into service. This dispute involved many genera in several fly families and created a pronounced polarity within the pipunculid community at the time. Hardy, Aczél, and Stone all advocated using the Meigen name *Dorilas* and indicated to the Commission that they and most other contemporary pipunculid workers such as Becker, Enderlein, Kertész, and Sack had been using this system for about 40 years (Aczél, 1951; Hardy, 1951a,b; Stone, 1951). However, there were several letters to the Commission and other published statements supporting the suppression of *Dorilas* Meigen, 1800 and validation of the name *Pipunculus* Latreille, 1802 (Collin, 1945; Oldroyd, 1951; Rapp, 1951; Smart, 1951). Despite the fact that the most productive pipunculid workers of the time supported the use of the name *Dorilas* over *Pipunculus*, the Commission made the decision based on usage in several families and ruled to suppress Meigen's 1800 publication (International Commission on Zoological Nomenclature, 1963).

The only other nomenclatural ruling that Hardy was involved in was a successful appeal to suppress the names *Prothechus* and *Alloneura* by Rondani and to place the names *Verrallia*, *Cephalosphaera* and *Tomosvaryella* on the Official List of Generic Names in Zoology (Hardy, 1958; International Commission on Zoological Nomenclature, 1961).

Hardy has had 1 subtribe, 1 genus, and 4 species of big-headed flies named in his honor [*Elmohardyina* Kuznetsov, *Elmohardyia* Rafael, *Cephalops hardyi* De Meyer, *Dorylomorpha hardyi* Albrecht, *Eudorylas hardyi* (Yang & Xu), and *Pipunculus hardyi* Rafael].

Hardy's Impact on Pipunculidae Taxonomy

In total, Elmo Hardy published 51 articles dealing with Pipunculidae between 1939 and 1989. Fig. 1 shows the accumulative species description curve for Pipunculidae in general and by Hardy. From this, it is clear that Hardy's impact was substantial from 1939 onwards. By 1972 he had doubled the number of described (and currently valid) species: from 292 known in 1938, he described an additional 320 (347 including synonyms ands subspecies).

Table 1 summarizes the number of species described prior to Hardy's work and his contribution, divided along zoogeographical regions. Table 2 presents the same data according to taxonomic genera recognized today (valid species only in both tables).

When taken per zoogeographical region (Table 1), his largest impact was on the Afrotropical region. From 17 valid species previously described from that region, he added 105. For the Neotropical fauna he tripled the number of known species during his active period, and for the Nearctic and Oriental faunas he doubled the number. Even when compared with the currently known valid species, Hardy described 70.5% of the Afrotropical fauna, while he accounts for 38.3, 31.8 and 29.3% respectively of the Nearctic, Oriental, and Neotropical faunas. From the Australasian/Oceanian fauna, Hardy described 30.2%, mostly from the Hawaiian Islands. His contribution is thus substantial for most zoogeographical regions, the only exceptions being the Palaearctic fauna with only 0.8% and the Australasian fauna. For the latter he never embarked on a program of study of the Australian fauna, which is poorly understood and apparently very species rich (Skevington, 1999, 2001, 2002). Additionally, articles by Hardy focusing solely on the Palaearctic fauna are few (see for example Hardy, 1967).

When examined along generic lines (currently accepted genera), a large difference in impact is noticed between the genera (Table 2). For the larger genera, his most significant impact is on *Cephalops* and *Eudorylas* with 40.2% and 29.1% respectively of the currently valid species. A lesser contribution was made to *Tomosvaryella* with 18.9%. For the smaller genera, Hardy described approximately half of the known valid species of the genera *Allomethus*, *Dasydorylas,* and *Microcephalops*. On the contrary, he had much less impact for *Dorylomorpha* (10.8%) and *Pipunculus* (5.6%). Also descriptions of *Chalarus*, *Jassidophaga*, and *Nephrocerus* are negligible. These genera have limited diversity outside the Holarctic; hence, he did not have such specimens in the extensive collections of Afrotropical, Neotropical, and Oriental faunas that he studied. In addition, a proportionally large part of the Holarctic species were described from the Palaearctic, leaving only a few new species for Hardy to describe from the Nearctic. The species complexity of some of these genera, such as *Chalarus*, was also only recently realized (Jervis, 1992).

However, his work was largely limited to the collections or geographical areas as discussed above. He never embarked on a systematic revision of any of the generic or suprageneric divisions recognized within the family. Also, type material of older described material was not always consulted or verified, especially for collections that were not readily available. For example, neither Becker's nor Loew's types were consulted during the revision of the Afrotropical fauna (Hardy, 1949c). Nevertheless, the number of species described by Hardy that are now synonymized is relatively low compared to the total number he described. Only 17 out of the 126 synonyms currently recognized are species described by Hardy.

Regarding higher classification, he mainly followed Aczél. Aczél (1940, 1948) published a framework for the family by erecting two main subfamilies: Chalarinae and Pipunculinae. The latter was divided into 2, and at a later stage 3 tribes: Nephrocerini, Protonephrocerini, and Pipunculini. Aczél also indicated which genera belonged to each of these taxa based on a phylogenetic tree he composed partly on *ad hoc* assumptions and partly on the study of the fossil record (Aczél, 1948).

Aczél also erected or discovered supporting evidence for the generic status of the several groups within the genus *Pipunculus*. These groups were first recognized by workers like Becker and accepted by subsequent researchers. Only in the 1940s were most of these groups given generic status by Aczél (1940), Enderlein (1936), and Collin (1945). Hardy followed this principle initially; however, in his later work (Hardy, 1953a) he considered some of these genera to be based on superfluous or too few characters and considered them merely as subgenera or entirely synonymous with *Pipunculus sensu stricto*. This was certainly a problem for Hardy as he again changed the status of some at a later stage. He had similar concerns for the status of *Jassidophaga*.

The evolution of his thoughts about higher classification can be followed through his catalogs of different zoogeographical regions that were published between 1965 and 1989. In his first catalog, covering the Nearctic region (Hardy, 1965c), he treated *Cephalops* as a synonym of *Pipunculus* s.s., *Eudorylas* and *Cephalosphaera* as subgenera of *Pipunculus*, and *Verrallia* and *Jassidophaga* as full genera. All genera of the Pipunculinae were treated within a single tribe, Pipunculini. A year later, in his Neotropical catalog (Hardy, 1966a), Tomosvaryellini was treated as a separate tribe from Pipunculini with *Tomosvaryella*, *Dorylomorpha* and *Allomethus* included in the former. In the Oriental (Hardy, 1975) and subsequent catalogs (Hardy, 1980, 1989), *Cephalops* was treated as a separate subgenus within *Pipunculus* and *Jassidophaga* was treated as a subgenus of *Verrallia*.

Contemporary Research

During Hardy's active period, only a few other researchers took up the study of Pipunculidae. The British workers J.E. Collin (e.g., 1920, 1937) and R.L. Coe (e.g., 1966a, b) worked on the Palaearctic fauna and K. Koizumi (1959, 1960) worked on species occurring in Asian paddy fields. For many years after 1972 this trend continued and there was little interest in taxonomic work on the group.

Taxonomic research accelerated again in the 1980s. Several researchers in different geographical regions initiated either regional faunistic studies or taxonomic revisions of particular groups. Regional revisions for the fauna of India (Kapoor *et al.*, 1987) and Japan (Morakote & Hirashima, 1990a–d; Morakote *et al.*, 1990a, 1990b) were produced. Kuznetzov described many Palaearctic species, predominantly from the former Soviet Republic States (e.g., Kuznetzov, 1990, 1991, 1994), while Rafael and co-workers revised the Neotropical fauna (e.g., Rafael, 1986a, 1986b, 1987a, 1987b, 1988; Ale Rocha & Rafael, 1995). Systematic revisions of several genera such as *Dorylomorpha* (Albrecht, 1990) *Chalarus* (Jervis, 1992), and *Cephalops* (De Meyer, 1989a, 1989b, 1990, 1992a, 1992b) were also produced in that period. Currently, the research continues with Skevington on the genus *Pipunculus* (Skevington & Marshall, 1998) and on the Australian fauna (Skevington, 1999, 2001, 2002), Földvári on Afrotropical Eudorylini, and a number of German workers (von der Dunk, Dempewolf, Kehlmaier). This surge has resulted in a dramatic increase in the number of described species (from 674 in 1972 to 1,343 in 2002; see Fig. 1).

Many of these revisions benefited from Hardy's pioneering work on these groups. His contributions often formed the basis for the work, despite his lack of comprehensive revisions. Early in his research, Hardy recognized the importance of male genitalic structures in the identification of Pipunculidae. He started including illustrations of these structures in his publications from 1943 onwards, although not always in a consistent way (for example, "*in situ*" views or the shape of syntergosternite 8 only). In many cases his descriptions and drawings are sufficient for recognition. Hardy also pointed out the importance of obtaining host records for pipunculid parasitoid species (Hardy, 1943). However, he did not engage in rearing himself but often noted homopteran species that were found in association with pipunculids as an indication of potential hosts. Even now, rearing records are scant and their presence would form an important asset in the study of this group. There is some indication that Pipunculidae tend towards oligophagy, attacking more than one species of host but showing a preference for a particular set of host species (Skevington, 2001). Part of this preference might be along generic lines.

Some of the issues raised by Hardy still form a topic of discussion among current pipunculid researchers. For example, the validity of species groups given generic rank based on the presence or absence of wing vein M_2 is still a source of discussion. In general, the work of D. Elmo Hardy on the dipteran family Pipunculidae can be considered fundamental and is the primary reference source for researchers today and in the future.

Acknowledgments

We thank Mihály Földvári (Hungarian Natural History Museum, Budapest) and Neal Evenhuis for commenting on drafts of the manuscript.

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D. Elmo Hardy Memorial Volume. Contributions to the Systematics and Evolution of Diptera. Edited by N.L. Evenhuis & K.Y. Kaneshiro.
Bishop Museum Bulletin in Entomology 12: 27–34 (2004).

Alishania, a New Genus with Remarkable Female Terminalia from Taiwan, with Notes on *Chrysotimus* Loew (Diptera: Dolichopodidae)

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Abstract

Alishania elmohardyi gen. & sp. nov. (Diptera: Dolichopodidae) is described from montane forests near 2400 m on Taiwan. This monotypic genus has an unusual enlargement of the female terminalia to form a large, rounded and laterally expanded sclerotized cavity whose function is unclear. *Alishania* is probably derived from *Chrysotimus* Loew, based on head shape, thoracic and leg setation, antennal structure, and venation. The cosmopolitan genus *Chrysotimus* is reviewed and suggested to be paraphyletic.

Introduction

This brief paper describes a distinctive new monotypic dolichopodid genus, *Alishania,* all specimens of which were collected near 2400 m in montane subtropical Taiwan. This genus has an unusual enlargement of the female terminalia, forming a rounded and laterally expanded sclerotized cavity.

The single included species, *Alishania elmohardyi,* is named in memory of D. Elmo Hardy in recognition of his work on the taxonomy of the Dolichopodidae, primarily as joint describer of 109 species of dolichopodids in his *Insects of Hawaii* (Hardy & Kohn, 1964). This new species has other connections to Hardy's work. It is part of the Oriental fauna, a focus of his taxonomic work on several fly families, as well as his scholarship as co-editor of *A Catalog of the Diptera of the Oriental Region.* Also, like much of the material Hardy studied, the specimens are part of the large holdings in the Bishop Museum, Honolulu.

Materials and Methods

This study is based on material housed at the Bishop Museum, Honolulu (BPBM) and the United States National Museum, Washington, D.C. (USNM). The morphological terminology follows McAlpine (1981). Measurements are in millimeters and were made on representative dry specimens. The position of features on elongate structures, such as leg segments, is given as a fraction of the total length, starting from the base. The relative lengths of the podomeres should be regarded as representative ratios and not measurements. The ratios for each leg are given in the following formula and punctuation: trochanter + femur; tibia; tarsomere 1/ 2/ 3/ 4/ 5. The following abbreviations and terms are used: I, II, III: pro- , meso-, metathoracic legs; C, coxa; T, tibia; F, femur; ac, acrostichal setae; ad, anterodorsal; av, anteroventral; dc, dorsocentral setae; dv, dorsoventral; hm, postpronotal setae; np, notopleural setae; pa, postalar setae; pd, posterodorsal; pm, presutural supra-alar setae; ppl, proepisternal setae; pv, posteroventral; sa, postsutural supra-alar setae; sr, presutural intra-alar setae.

Genus *Alishania* Bickel new genus

Type species: *Alishania elmohardyi* Bickel,new species.

Diagnosis: Length: 2.2–2.4; major head, thoracic and leg setae yellow; dorsal postcranium distinctly convex; face and clypeus wide with sides parallel; pedicel short subtriangular; mesonotum anteriad of scutellum distinctly flattened; ac absent; lateral scutellar setae absent; legs yellow; FII and FIII with strong anterior subapical seta; wing distinctly longer than body; crossvein h present only as trace;

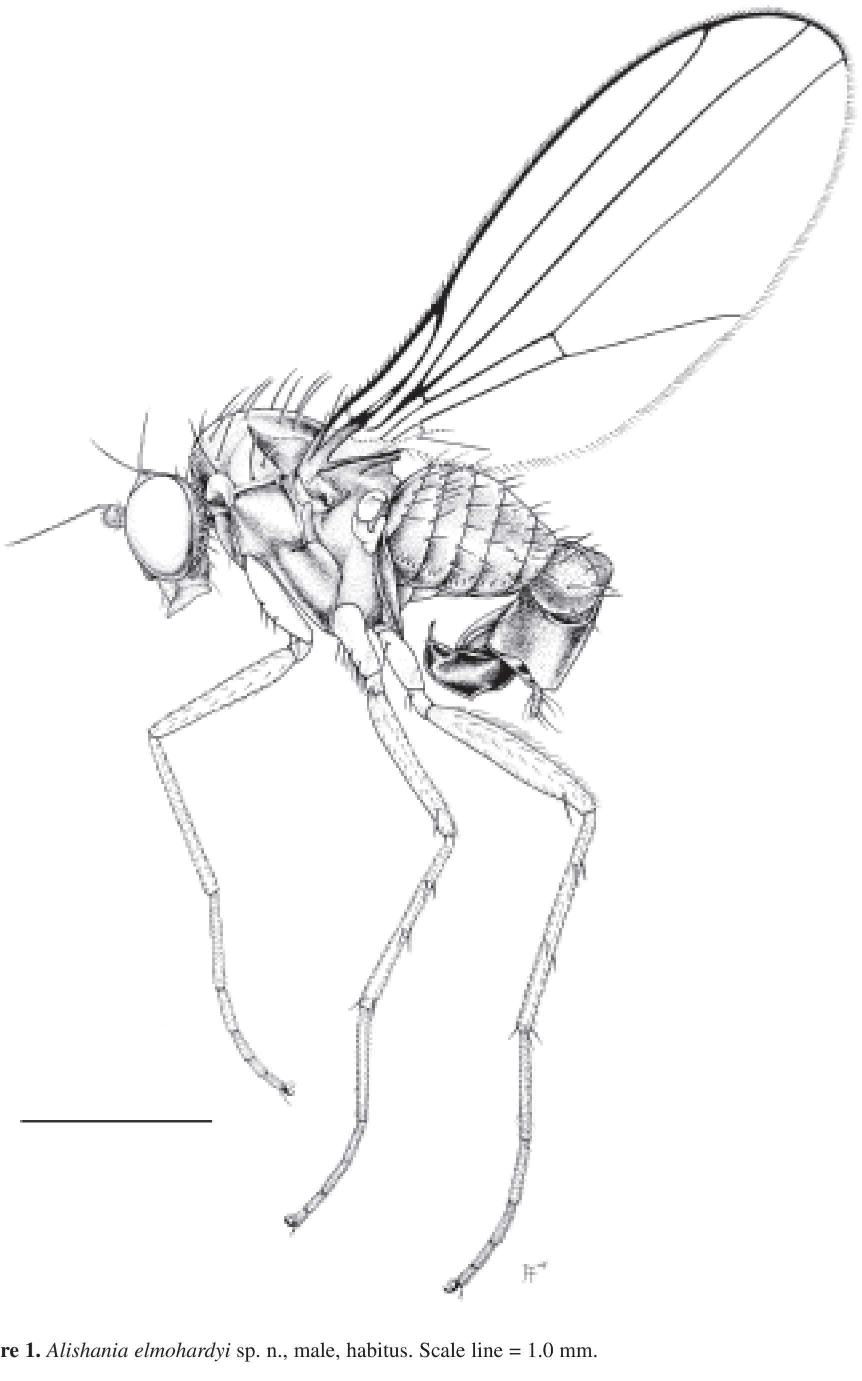

Figure 1. *Alishania elmohardyi* sp. n., male, habitus. Scale line = 1.0 mm.

R_{4+5} and M parallel to apex; M without *bosse alaire*; surstlyus massive and curved, apically pointed with some short setae; female terga 3 and 4, and most sterna yellow; female tergum 8 greatly enlarged and laterally expanded, forming large hollow sclerotised chamber, externally glabrous.

Etymology: *Alishania* is derived from Alishan, a locality in Taiwan where all specimens of the single included species were collected. The gender is feminine.

Alishania elmohardyi Bickel, **new species**

(Figs. 1–3)

Description. **Male** (Fig. 1): length: 2.2–2.4; wing: 2.6 × 1.2.

Head: vertex, frons, and face metallic blue-green and covered with dusting of grey pruinosity; major setae yellowish; strong verticals and strong diverging ocellars present; 2 short postverticals present on dorsal postcranium; dorsal postcranium distinctly convex, so that head appears free from thorax; 7–8 postorbitals present; eye facets of uniform size; face and clypeus wide with sides parallel, and eyes distinctly separated; palp yellow with whitish pruinosity; proboscis brown; antenna dark brown; postpedicel short subtriangular; arista dorsal, and slightly longer than head height.

Thorax: mostly metallic green with dusting of grey pruinosity, except brownish adjacent to coxa II, and metepimeron mostly brownish but infuscated dorsally; setae yellow; posterior mesonotum anteriad of scutellum distinctly flattened; ac absent; 6 strong dc present; 1 pa, 2 sa, 2 sr, 2 npl, 1 hm, 1 pm present; median scutellars strong, laterals absent.

Legs: coxae and remainder of legs yellow; setae yellow; CI and CII with yellow anterior hairs, and CIII with lateral seta; I: 3.0; 3.0; 1.5/ 0.7/ 0.5/ 0.5/ 0.4; leg I without outstanding hairs or setae; II: 3.5; 3.7; 2.0/ 0.8/ 0.5/ 0.3/ 0.4; FII with strong anterior subapical seta and weak av seta just distad, and no posterior subapical seta present; TII with offset ad-pd setal pairs at 1/4, and 2/5, and subapical av and pv setae; III: 3.5; 4.2; 1.8/ 1.0/ 0.6/ 0.4/ 0.4; FIII with strong anterior subapical seta and weaker av seta both at 4/5, but no posterior subapical setae present; TIII with offset ad-pd setal pairs near 1/4 and 2/3.

Wing: hyaline with veins yellow; Sc fusing with R_1; crossvein h present only as pale trace; R_{2+3} long, joining costa in distal sixth of wing; R_{4+5} and M parallel to apex; M without bosse alaire; anal vein short; CuAx ratio: 0.2; lower calypter yellow with fan of yellow setae; halter yellow.

Abdomen: preabdomen metallic green with short yellowish vestiture; segment 7 short; sternum 8 forming cap over rather small hypopygial foramen, which is left lateral in position; hypopygium (Figs. 3a,b) dark brown, massive; epandrium subrectangular; hypandrium curved and with distal rough surface; aedeagus with curved pointed projections, and asymmetrical in ventral view (Fig. 3b); surstlyus massive and curved, apically pointed with some short setae, and asymmetrical, with right surstylus distinctly larger than left; cercus short and blunt.

Female: (Fig. 2) similar to male except as noted: distinctly larger, wing length 2.9 × 1.2; face only slightly wider; abdominal terga 1 and 2 metallic green, although tergum 2 yellow laterally; terga 3 and 4 yellow; sterna 1–6 yellow; 5–7 dark brown-metallic green; segment 8 (Figs. 3c, d) greatly enlarged and laterally expanded, forming large hollow sclerotized chamber, externally dark brown and glabrous; tergum 9 forming downflexed extension of tergum 8, and with long setae; cercus short.

Type material. Holotype ♂ (BPBM 16, 512), Paratypes, 47 ♂, 43 ♀: **TAIWAN**: Alishan, Chiayi Hsien, 2400 m, 12–16.vi.1965, T Maa & K.S. Lin (BPBM).

Additional material. **TAIWAN**: ♂, “Arisan [sic.], Formosa”, 4.vi.1932, J.L. Gressitt (USNM).

Remarks. *Alishania* is a monotypic genus comprising *A. elmohardyi,* sp. n., known only from the type locality at 2400 m in Alishan, Taiwan. Hsieh *et al*. (1997) provided a summary of the montane forest vegetation of Taiwan, and Alishan at 2400 m is probably within the upper *Quercus* zone, a moist montane evergreen broadleaf forest. *Alishania* is possibly endemic to Taiwan.

The female terminalia of *Alishania* requires discussion. Although the male hypopygium is rather large, other dolichopodid taxa (e.g., some Dolichopodinae, some Sciapodinae, *Babindella*) also have developed enlarged hypopygia (sometimes almost equal in size to the preabdomen), without any corresponding modification of the female terminalia. In female *Alishania,* the greatly

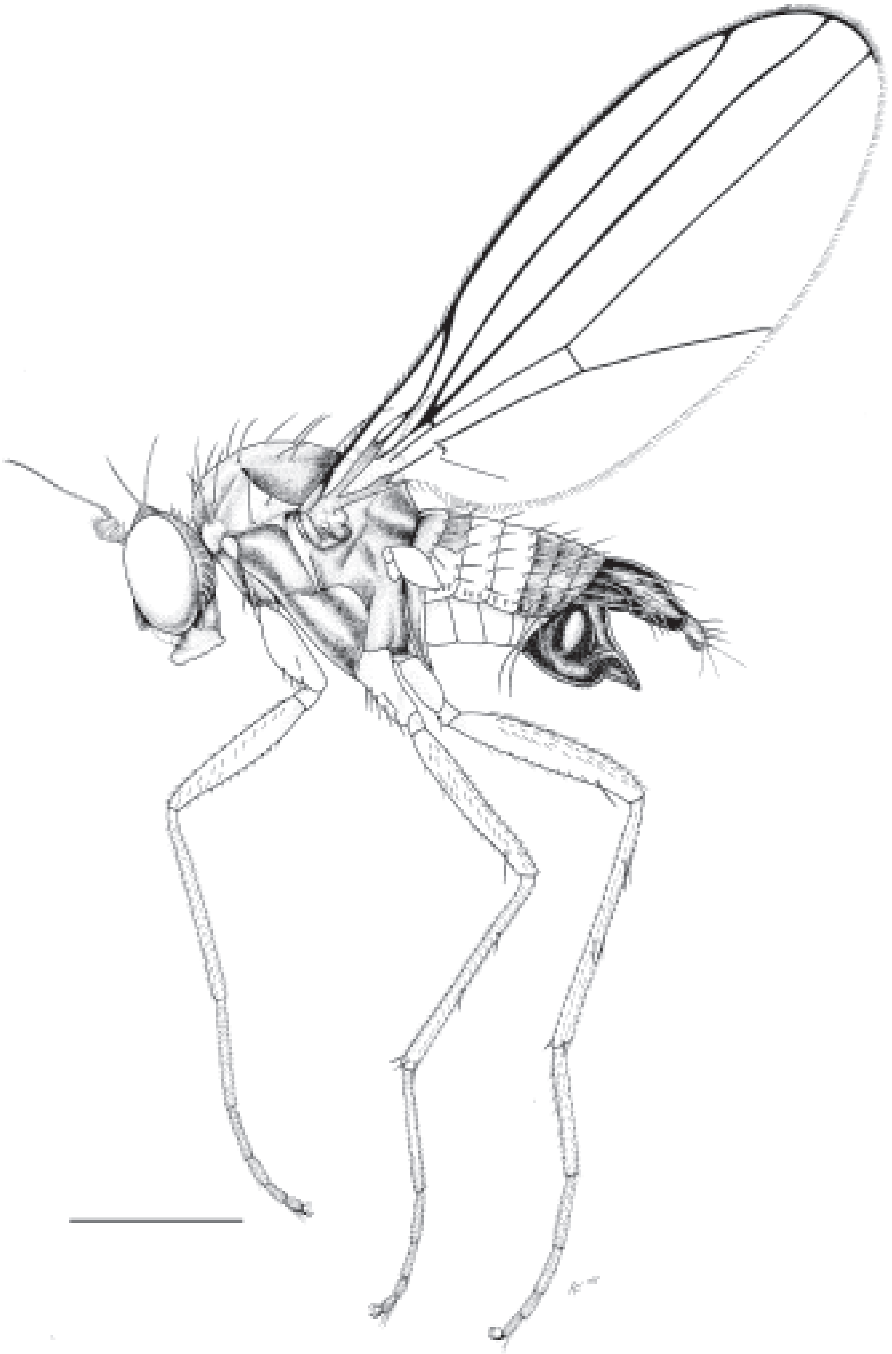

Figure 2. *Alishania elmohardyi* sp. n. female, habitus. Scale line = 1.0 mm.

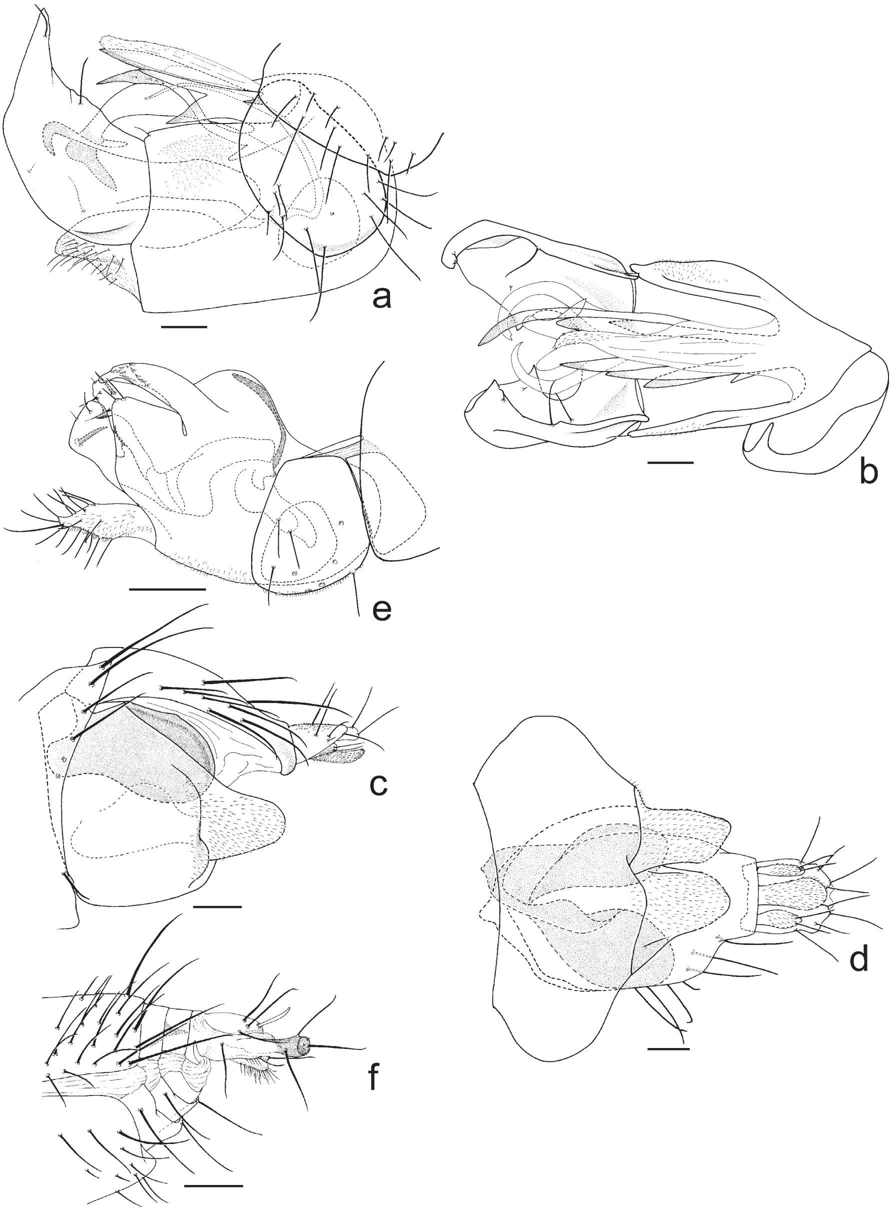

Figure 3. *Alishania elmohardyi* sp. n.: **a**. hypopygium, left lateral; **b.** hypopygium, ventral; **c.** female oviscapt, left lateral; **d**. female oviscapt, ventral. *Chrysotimus pusio* Loew: **e**. hypopygium, left lateral; **f**. female oviscapt, left lateral. Scale line = 0.1 mm.

enlarged and laterally expanded sclerotised chamber formed by segment 8 is striking (Fig. 2). What is the function of this chamber? Is it solely for receiving the large hypopygium during mating, or might it have a possible brooding function? These questions cannot be answered without study of the species' biology. However, the extreme morphology of the *Alishania* female terminalia almost brings to mind a "hopeful monster" explanation for this modification.

Phylogenetic Relationships

What are the phylogenetic relationships of *Alishania*? Apart from the enlarged male hypopygium and the highly modified female terminalia, it shares many characters with the cosmopolitan genus *Chrysotimus* Loew, and probably is directly derived as a local endemic from this genus (see below for a discussion of the genus *Chrysotimus* and its paraphyly).

I. Characters shared by *Alishania* and *Chrysotimus* (not necessarily derived).

Postpedicel subrectangular with dorsal arista.
Postcranium strongly convex
Face subequal and parallel sided in both sexes.
Posterior mesonotum strongly flattened
Lateral scutellar setae reduced to tiny setae or absent.
Legs without strong male secondary sexual characters
Leg I without major setae, and tibia I without distal ad serration of short setae.
Femora II and III with anterior preapical setae
Tibiae II and III with ad and pd setae, often as offset pairs.
Wings very long, least one-quarter longer than body length in both sexes (apart from many hydrophorine genera and *Campsicnemus* spp., in most Dolichopodidae, wing and body length are subequal).
R_{4+5} and M and distinctly parallel.
M straight, without any trace of flexion or *bosse alaire*.
Humeral crossvein (h) very faint reduced to lost.
With very long distal CuA (CuAx ratio very low).
Abdomen often with two or more bright yellow terga, especially in females, which are sometimes also present in conspecific males.
Females distinctly larger than males.

II. Autapomorphies of *Alishania* (with respect to *Chrysotimus)*

Hypopygium greatly enlarged with massive curved surstyli
Aedeagus, asymmetrical with curved pointed projections.
Female terminalia with greatly enlarged and laterally expanded sclerotised chamber formed by segment 8.

Notes on *Chrysotimus* Loew and related genera

Diagnosis: Genus *Chrysotimus:* rather small (1.8–3.2 mm wing length) and stout bodied flies with wings distinctly longer than body; major head, thorax and leg setae often yellow or brownish with yellow reflections.

Head : spheroidal, not much higher than wide; dorsal postcranium convex; vertex not excavated; scape dorsally bare; face bare of setae; eye not strongly ovate, but almost circular; face parallel sided, and of subequal width in both sexes; arista dorsal to apical on subtriangular postpedicel.

Thorax: metallic green; rather broad, not elongate; posterior mesonotum distinctly flattened and slightly depressed between dc setae, and distinct from curved anterior mesonotal surface; ac biseriate or absent; scutellum with one pair marginal setae only, or sometimes with short weak lateral setae.

Legs. often mostly yellow in color; tibia I without ad setal serration; femora II and III with anterior preapical setae, and with weaker preapical pv setae; tibia II and III with ad and pd setae, often as offset pairs.

Wing; at least 1/4 longer than body length in both sexes; wing rather broad, and rectangular in shape; R_{4+5} and M each straight and distinctly parallel; M without any trace of flexion or *bosse alaire.*

Abdomen. often with 2 or more bright yellow terga, especially in females, which are sometimes also present in conspecific males.

Male hypopygium (Fig.1e, *C. pusio* Loew, type species of genus) either encapsulated or slightly pedunculate; abdominal segment 7 (peduncle) with distinct tergum and sternum, never greatly prolonged; sternum 8 large, ovate, covering hypopygial foramen on left side; hypopygial foramen left lateral in position and small, almost circular; epandrium rather massive; hypandrium fused to capsule at base; surstyli broad and fused to epandrium, and with medially directed setae and projections; cercus short, digitiform.

Female (Fig. 1f, *C. pusio,* type species); tergum and sternum unmodified, bare; tergum 9 split medially into two hemitergites, and with long setae and pale blade-like seta as shown; cercus elongate and digitiform, with setae as shown.

Remarks. Most *Chrysotimus* species are less than 2.0 mm long, usually without prominent male modifications, and are often overlooked or relegated to some small-sized "*Chrysotus*-like" residue. Additionally, the tendency of specimens to collapse when dry mounted has not increased their attractiveness to being studied. Apart from commonly being included with *Chrysotus* in collections, *Chrysotimus* has been mistaken for, and even described as *Thrypticus* Gerstäcker (Medeterinae) primarily because of its often yellow setae, depressed posterior mesonotum, and bright metallic green color.

Chrysotimus is almost cosmopolitan, and occurs primarily in temperate and upland tropical moist forests. In tropical Costa Rica, for example, *Chrysotimus* is known only from forests above 1500 m (the occurrence of *Alishania* in montane forests near the Tropic of Cancer in Taiwan is not inconsistent with being derived from *Chrysotimus*). The genus is particularly diverse in the southern hemisphere temperate forests of Australia/ Tasmania, New Zealand, New Caledonia, and Patagonia, where large numbers are often collected in yellow pans and Malaise traps. However, these southern *Chrysotimus* faunas are poorly known. To date, 37 *Chrysotimus* species have been described, a fraction of the true number: Australasia (13), Orient (2), Afrotropics (0), Palaearctic (8), Nearctic (7), and Neotropical (7). I have also seen undescribed species of this genus in Baltic Amber inclusions.

Although *Chrysotimus* had been placed in the Sympycninae, Robinson (1970) referred it to the Peloropeodinae, a subfamily that comprises a number of small-sized genera that mostly share a flattened posterior mesonotum, veins R_{4+5} and M parallel, and with anterior preapical setae present on femora II and III. However, the male postabdomen of included genera display varied morphology, suggesting the subfamily is a heterogeneous assemblage.

As discussed above, *Chrysotimus* is the most probable ancestor and therefore paraphyletic with respect to *Alishania.* In addition, *Chrysotimus* is probably paraphyletic with respect to several other genera of limited distribution. Such paraphyly must be accepted, and indeed it often *is*, at least tacitly, for many large complex insect genera. *Chrysotimus* is a cosmopolitan genus with a rich but poorly known fauna that dates to at least the geological period of Baltic Amber (Eocene-Oligocene). It therefore is not surprising that such a genus has served as a paraphyletic "mother taxon." Many complex cosmopolitan genera are likely to be paraphyletic with respect to derived daughter taxa in just such a matter. At this stage it is premature to split *Chrysotimus* for several reasons, not the least of which is retaining the overall internal unity that allows the genus to be recognized and keyed.

The following genera are allied to *Chrysotimus*:

1. *Alishania* gen. nov, a monotypic genus restricted to montane Taiwan (described above).
2. *Nanomyina* Robinson. This monotypic genus comprises *N. barbata* (Aldrich), known from marine littoral habitats in eastern USA, the Caribbean, and Pacific Mesoamerican coast. It has a row of setae near clypeus in both sexes (autapomorphy).
3. *Fedshenkomyia* Stackelberg, a monotypic genus restricted to Turkistan. I have not seen specimens of this genus, but Negrobov (1968) illustrated the hypopygium of *F. chrysotimiformis* Stackelberg.

4. *Guzeriplia* Negrobov, a genus with two species restricted to the Caucasus. I have seen a male paratype (USNM) of *G. chlorina* Negrobov, and although the specimen is collapsed, it has the overall habitus and characters of *Chrysotimus,* including long pale yellow setae on the head and thorax, biseriate ac, and scutellum with strong median seta and short side hairs. It is distinguished by a rather bulbous hypopygium with elongate surstyli and cerci, as figured in Negrobov (1968). *Guzeriplia* is within the range of variation in *Chrysotimus,* and probably needs to be placed in synonymy.

Acknowledgments

I thank Gordon Nishida and Neal Evenhuis (BPBM) and Chris Thompson (USNM) for the loan of specimens. Hannah Finlay drew the figures.

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Humongochela, a New Genus of Waterfall-Loving Flies From the Marquesas Islands (Diptera: Dolichopodidae)

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Abstract

A new genus of Dolichopodidae allied to *Campsicnemus*, *Humongochela*, **n. gen.**, is described to include three new species: *H. englundi* **n. sp.**, *H. hardyi* **n. sp.**, and *H. polhemusi* **n. sp.** A key to species in the genus is given and all species are described and illustrated. These flies are found only in association with vertical rock surfaces near waterfalls in the Marquesas Islands.

Introduction

Little is known of the dolichopodid fauna of the Marquesas and few collecting ventures have taken place in which to ascertain the fauna of these flies that abound in those remote French Polynesian islands. However, two recent scientific expeditions led by the Smithsonian Institution and the Bishop Museum have resulted in several new discoveries of aquatic insects and have helped significantly increase our knowledge of the biodiversity of these islands. Some of these results included recent discoveries of 3 species of water-skating *Campsicnemus* Haliday, which were published in Evenhuis (2000). However, many more new *Campsicnemus* from the Marquesas await description and publication. In the meantime, this paper describes a remarkable new genus of sympycnine Dolichopodidae occurring on Nuku Hiva, Fatu Hiva, and Hiva Oa that resembles an extremely large *Campsicnemus*.

With the publication of the three new species in this genus, the Marquesan dolichopodid fauna is now known from 10 species in 6 genera (*Condylostylus*, *Chrysosoma*, *Medetera*, *Campsicnemus*, *Chrysotus*, *Humongochela*, n. gen.). Based on specimens at hand, it is estimated that an additional 10–15 species of dolichopodids await description from these islands, primarily in the genus *Campsicnemus*.

Materials and Methods

Specimens for study derived from the Bishop Museum, Honolulu (BPBM) and the National Museum of Natural History (USNM). When series number allowed, specimens were distributed to the following institutions: Museum National d'Histoire Naturelle, Paris (MNHN), Laboratoire d'Entomologie Médicale, Institut Louis Malardé, Paea, Tahiti (ILMP). Morphological terminology follows Evenhuis (1997).

Systematics

Humongochela Evenhuis, **new genus**

Type species: *Humongochela hardyi* Evenhuis, new species, by present designation.

Diagnosis. Relatively large sympycnine dolichopodids (ca. 5 mm in length) very similar in appearance to large species of *Campsicnemus* with pronounced modifications of the midleg. The genus is easily distinguished from *Campsicnemus* by crossvein m-cu subequal in length to last section of vein CuA_1 from crossvein m-cu to wing margin (the crossvein m-cu less than 1/2 the length of the last segment of CuA_1 in *Campsicnemus*) and the large claws (1/2 length of last tarsomere) (slightly less

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1. Contribution No. 2003-005 to the Pacific Biological Survey.

Figure 1. *Humongochela polhemusi*, male habitus

than 1/3 the length of the last tarsomere in *Campsicnemus,* but 1/8 the overall size of those in *Humongochela* — compare Figs. 10 and 11).

Description. **Male** (Fig. 1). *Head*. Fairly large, in lateral view slightly smaller in size than thorax. In frontal view with eyes slightly converging below level of antennal sockets, then diverging again to level of clypeus; width of front at narrowest portion about equal to width of two ommatidia. Ocellars strong, diverging, subequal to or slightly shorter than length of antennal segments (without arista). Antenna (Fig. 6) with scape cylindrical, length ca. 2 × width; pedicel short cup-like, with short stiff setae dorsally; first antennal flagellomere relatively long, subequal in length to scape and pedicel together, subtriangular in shape; arista pubescent, subequal in length to head height. Mouthparts large, extending below eyes in lateral view.

Thorax. Black to dark brown dorsally, with blue-green reflections in some specimens. With following compliment of setae: 4-5 *dc* (with posteriormost *dc* diverging from line of others); 1 *np*; 1+2 *ph*; 1+1 *sa*; 1 *pa*; 1+1 *sc*; *ac* absent. Scutellum with 1+1 *sc*, where smaller hair-like setae is lateral; posterior margin with 4 tiny hairs medially. Pleura with upper sclerites brown to black, lower sclerites varying in coloration.

Legs. CI with apical comb of 6 stiff black bristles, 2 subapical bristles, numerous smaller setae on anteroapical half. CIII with 3–4 very tiny hairs on lateral surface. FI and FII subequal in length;

FIII 1.3 × length of FII. TI and TII subequal in length to FI and FII; TIII long, 1.5 × length of FIII. FII, TII, and IIt1 with MSSC (Figs. 7–9). Fore and hind tarsi normal; mid basitarsus (IIt1) modified with apical thorn-like spur apically; IIt2 inserted either apically or subapically on IIt1. Claws extremely long, thin, length about 1/2 length of last tarsomere (Fig. 10). Empodium feather-like, subequal in length to claws; pulvilli reduced, ca. 1/4 length of claws.

Wing (Fig. 1). Long, slightly shorter than body length. Veins R_{4+5} and M_1 straight, converging slightly at wing margin. Cell cup incomplete. Crossvein m-cu subequal to or longer than last section of CuA1. Vein CuA_1 not quite reaching wing margin. Halter length subequal to length of CIII, with a few tiny hairs at base of knob.

Abdomen. Long, thin, width subequal to that of thorax. Tergite II with patch of stiff black setae posterolaterally, tergite II with fewer such hairs; otherwise dorsum of abdomen covered with sparse short hairs.

Genitalia. Hypopygium much like in *Campsicnemus*: small without differentiating features. Surstyli small, blunt, dark brown. Aedeagus sinuous, extending beyond hypopygial capsule for length subequal to hypopygium.

Female. Similar to make except for lack of MSSC and with a short, stubbier subconically shaped first antennal flagellomere. Oviscapt with 3 pairs of short stubby acanthophorites.

Remarks. This genus is found on 3 islands of the Marquesas (Fatu Hiva, Nuku Hiva, and Hiva Oa) (Fig. 2) with one species on each. All are found on vertical surfaces (i.e., seeps or rocks) near waterfalls. It is presumed that the long claws and extremely reduced pulvilli are evolutionary adaptations to allow a better grip on the otherwise slippery substrata near these swift moving waters.

Only three species are known thus far and it is possible that additional species may be found on other Marquesan islands with waterfalls in between Nuku Hiva and Hiva Oa (namely, Ua Pou, Ua Huka, and Tahuata).

Etymology. The generic name derives from the American slang “humongous”, meaning large, monstrous + “*chela*” Latin = claw; referring to the extraordinary development of the tarsal claws.

Classification. The genus is placed in the Sympycninae, where it fits with characters it has in common with *Campsicnemus* including antennal shape, male genitalia, and MSSC of the male midleg. More study will need to be done on the subfamilial limits of Sympycninae and related subfamilies in order to properly ascertain the true subfamilial placement of this and other related genera.

KEY TO SPECIES OF *HUMONGOCHELA* EVENHUIS BASED ON MALES

1. Crossvein m-cu subequal in length to last section of CuA_1 from crossvein m-cu to wing margin; claws 1/2 length of last tarsomere .... **Humongochela** Evenhuis, **n**. **gen**.

–. Crossvein m-cu less than 1/2 length of distance of last segment of CuA_1; claws small, 1/8 to 1/10 length of last tarsomere .... **Campsicnemus** Haliday

2. Mid tibia with prominent bulge on apical third, narrowed distally; bulge with dense tuft of fine wavy setae (Fig. 7) ... (Nuku Hiva) .... **hardyi** Evenhuis, **n**. **sp**.

-. Mid tibia inflated apically (Figs. 8,9), without prominent bulge but gradually expanding to apex 3

3. Lower pleura yellow, concolorous with fore coxae; TII with apical bristles subequal in length to baistarsus (Fig. 8) ... (Fatu Hiva) .... **englundi** Evenhuis, **n**. **sp**.

-. Lower pleura brown, concolorous with upper pleura; TII with apical bristles 1/4 length of basitarsus (Fig. 9) ... (Hiva Oa) .... **polhemusi** Evenhuis, **n**. **sp**.

Humongochela hardyi Evenhuis, **new species**

(Figs. 7, 10)

Diagnosis. Differs from the other species in this genus by the pronounced bulge on the mid tibia in the male and the longer basitarsus (the other two species in the genus have the mid tibia without such a bulge and the basitarsus shorter in length).

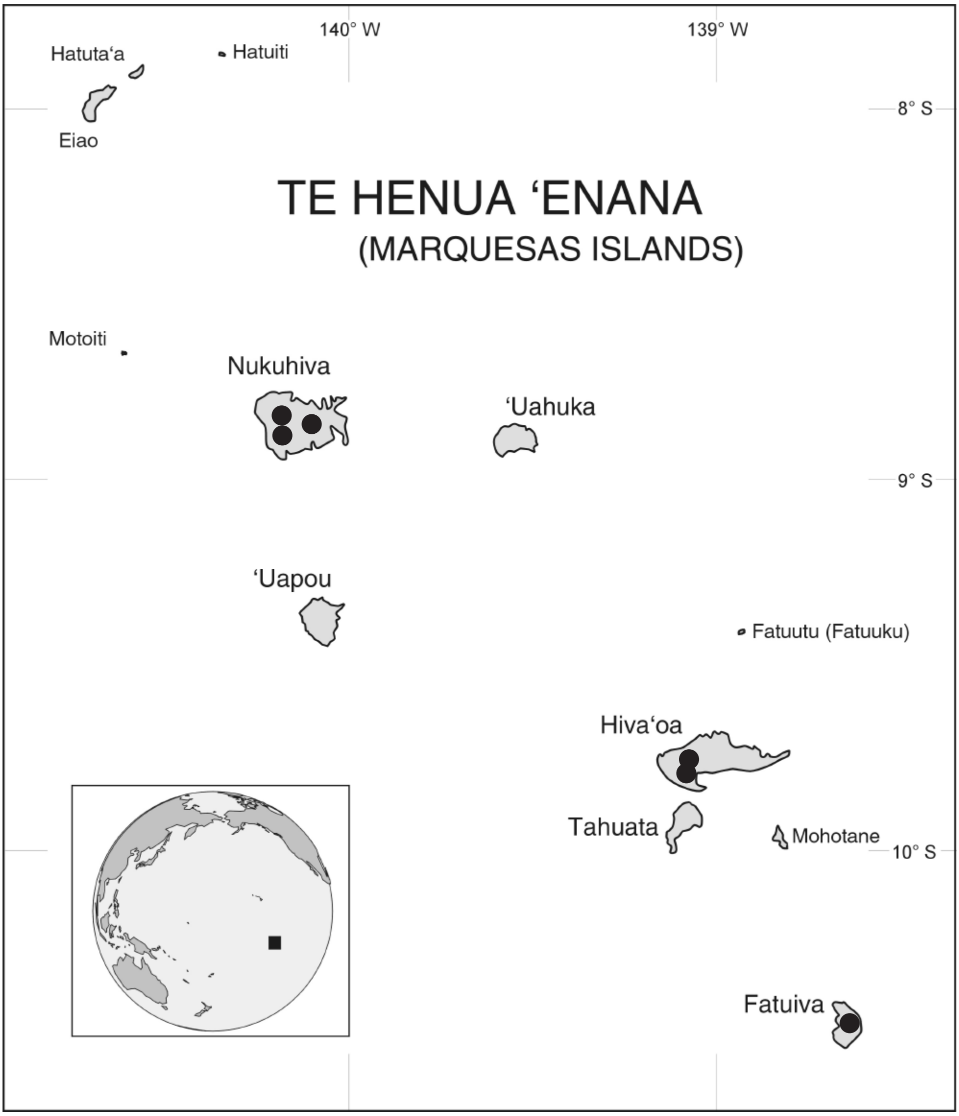


Figure 2. Map of the Marquesas showing distribution of species of *Humongochela* (black dots).

Male. Body length: 5.6–5.8 mm. Wing length: 5.0 mm. *Head*. Gray-black; inner eye margins parallel-sided from level of antenna to level of upper margin of clypeus; palp and proboscis brown; antenna dark brown with arista length slightly less than head height.

Thorax. Mesoscutum, scutellum, and upper pleura dark brown; lower pleura (katepisternum, meron, katepisternum) yellow; dorsocentrals with last pair diverging posteriorly; thoracic setae black to dark chocolate brown: 5 *dc*; 1 *np*; 1+2 *ph*; 1+1 *sa*; 1 *pa*; 1+1 *sc*; *ac* absent.

Legs. CI and CIII yellow, CII yellow anteriorly, brown posterolaterally; Femora yellow, brown at extreme apex, apical brown color most evident on mid and hind femora. It4 with large apical spurs ca. 1/2 length of tarsomere; claws large, ca. 1/2 length of It5; otherwise fore leg unmodified and without MSSC. FII (Fig. 7) with 6–7 long stiff black setae ventrolaterally on basal 1/3, numerous shorter, almost peg-like black setae extending further along ventral surface to subapex; ventroapex without setae. TII (Fig. 7) sinuous, flared from base to apex, with swollen bulge just beyond middle; 5 strong black setae on lateral surface just before bulge; numerous admixed long and midsized setae along ventral mesal surface; bulge with dense tuft of long fine wavy setae mixed with long stiff black setae. IIt1 1/2 length of IIt2, with thorn like apical spur, IIt2 inserted subapically; IIt4 with large apical spurs 1/2 length of tarsomere; claws (Fig. 10) large, 1/2 length of IIt5, pulvilli small, 1/4 length of claws; otherwise IIt2-5 unmodified. FIII with numerous short spine-like setae along entire ventral surface, longest basally, becoming shorter apically; claw shorter than on fore and midlegs, ca. 1/3 length of IIt5.

Wing. Subhyaline throughout; vein M_1 slightly converging with R_{4+5} at wing margin; crossvein m-cu slightly longer than last section of CuA_1; CuAx 0.80; CuA_1 almost reaching wing margin; halter dark brown at extreme base, otherwise bright white.

Abdomen. Dark brown dorsally with yellow brown anterolaterally; stiff black setae posterolaterally on tergite I. Hypopygium light brown; apex of surstyli dark brown; cerci brown.

Female. As in male except as follows: body all black with blue-green reflections. First antennal flagellomere short, subconical. Wing smoky brown, especially along longitudinal veins. Pleura brown. Legs brown, trochanters paler. Claws on all legs subequal in length; otherwise legs without modifications or MSSC.

Types. Holotype male (BPBM 16,507) and paratypes (4 male, 3 female) from **MARQUESAS**: Nuku Hiva: Taipi Valley, Tehua Falls, 500 ft., 22.viii.2001, below second falls, cascade/pool, 8°52'14" S, 140°06'16" W, R.A. Englund. *Other paratypes*: Nuku Hiva: 1 male, Vaikaheke Stream, 2100 ft., 20.x.1999, tributary to Upper Vaiohei Valley, riffle, splash zone, 8°53'27" S, 140°08'39" W, R.A. Englund (BPBM); 1 male, same locality, 18.x.1999, caught on vertical wet rock face, D.A. Polhemus (USNM); 2 females, same locality, 18.x.1999, 620 ft., R.A. Englund (BPBM); 1 male, 1 female, Toovi Plateau, stream, 2800 ft., 23.viii.2001, headwall falls, along seep, 8°50'58.1" S, 140°09'14.5" W, R.A. Englund (BPBM). Holotype in BPBM. Paratypes collected with holotype in BPBM, USNM, and MNHN.

Habitat. Occurring on vertical surfaces of rocks and seeps in association with falls (Fig. 4).

Etymology: This species is named for D. Elmo Hardy, who provided this author with encouragement and wise advice as well as numerous inspirational stories associated with working with Dolichopodidae in Hawai‘i.

Humongochela englundi Evenhuis, **new species**

(Fig. 8)

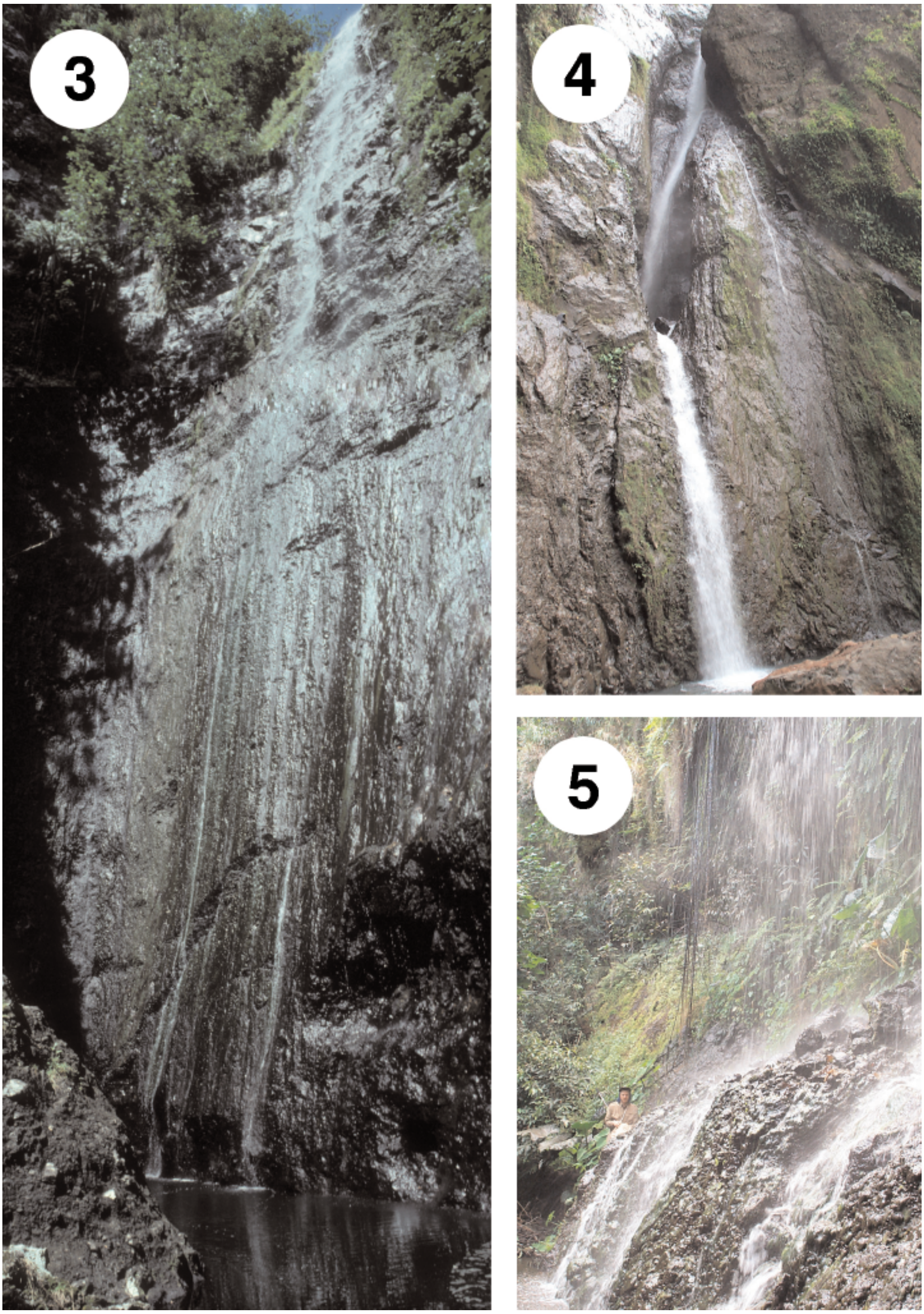
Diagnosis. Most similar to *H. polhemusi*, from which it can be separated by the short apical tibial spurs ca. 1/4 length of basitarsus (these spurs ca. 2/3 length of basistarsus in *H. polhemusi*) and the predominantly yellow lower pleura (katepisternum, meron and katepimeron) (these sclerites brown in *H. polhemusi*).

Male. Body length: 5.6–5.8 mm. Wing length: 5.0 mm. *Head*. Gray-black; inner eye margins parallel-sided from level of antenna to level of upper margin of clypeus; palp and proboscis brown; antenna dark brown with arista length slightly less than head height.

Thorax. Mesoscutum, scutellum, and upper pleura dark brown; lower pleura (katepisternum, meron, katepisternum) yellow; dorsocentrals with last pair diverging posteriorly; thoracic setae black to dark chocolate brown: 5 *dc*; 1 *np*; 1+2 *ph*; 1+1 *sa*; 1 *pa*; 1 + 1 *sc*; *ac* absent.

Legs. Coxae yellow. Femora yellow, brown at extreme apex, apical brown color most evident on mid and hind femora. It4 with large apical spurs ca. 1/2 length of tarsomere; claws large, ca. 1/2 length of It5; otherwise fore leg unmodified and without MSSC. FII (Fig. 7) with two rows of 6–7 long stiff black setae ventrally on basal 1/2, numerous shorter, peg-like black setae extending further along ventral surface to apical 2/3; ventroapex with 4 small peg-like setae. TII (Fig. 7) as in *H. polhemusi* except more numerous setae at apical 1/3 of lateral surface; apical tibial spurs 1/4 length of IIt1.

Wing. As in *H. polhemusi*.



Figures 3–5. Type localities of *Humongochela*. **3**. Fatu Hiva, Upper Hanavave Stream, 400–500 ft. elev., cascade (type locality of *Humongochela englundi*). **4**. Nuku Hiva, Taipi Valley, Tehua Falls, 500 ft. elev., cascade/pool (type locality of *Humongochela hardyi*). **5.** Hiva Oa, Atuona Valley, Vaioa River, 1050 ft. elev., cascade (type locality of *Humongochela polhemusi*).

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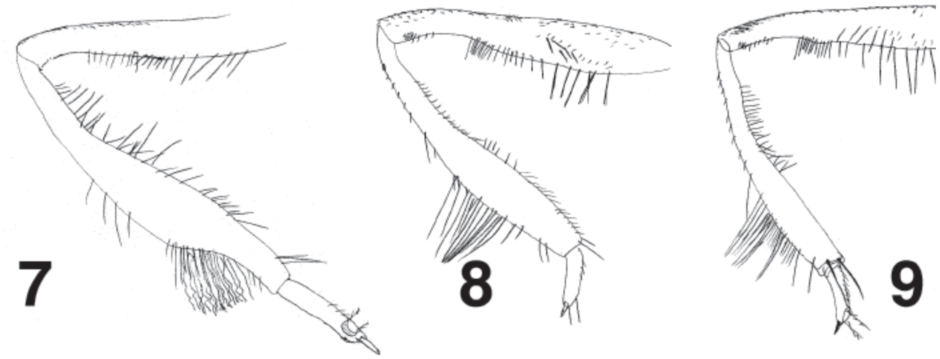

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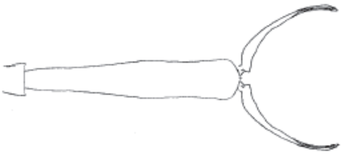

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Figure 6. *Humongochela polhemusi*, antenna. **Figures 7–9**. *Humongochela* male mid femora, tibiae, and basitarsi. **7**. *H. hardyi*. **8**. *H. englundi*. **9**. *H. polhemusi*. **Figure 10**. *Humongochela hardyi*, last tarsomere and claw of male midleg**. Figure 11.** *Campsicnemus scurra*, last tarsomere and claw of male midleg (Figs. 10 and 11 drawn to same scale).

Abdomen. Black with paler areas laterally on tergites; stiff black setae posterolaterally on tergite I. Hypopygium yellow; apex of surstyli dark brown; cerci yellow.

Female. As in male except as follows: Pleura and coxae yellowish brown. First antennal flagellomere short, conical, but longer than in *H. hardyi* or *H. polhemusi*. Wing infumate brown, especially so along longitudinal veins. Halter stem gray-brown, knob white.

Types. Holotype male (BPBM 16,508) from **MARQUESAS**: Fatu Hiva: Hanavave, Upper Hanavave Stream, 400–500 ft. cascade face, 10°30’31.3”S, 138°39’45.7”W, 27.viii.2001, R.A. Englund. Paratype female from same locality except D.A. Polhemus collector (USNM). Holotype in BPBM. Paratype in USNM.

Habitat. Only a single male and female of this species were collected from the cascade face of Upper Hanavave Stream on Fatu Hiva (Fig. 3).

Discussion. This is the only species in the genus that has females that are similar in general appearance to the males. The other 2 species have almost black females, while the males are brown and yellow colored.

Etymology: This species is named for Ronald Englund, avid participant in these expeditions, superb collector of aquatic insects, and the one who collected the only male of this species.

Humongochela polhemusi Evenhuis, **new species**

(Figs. 1, 5, 6, 9)

Diagnosis. Can be distinguished from the congeners by the dark lower pleura in combination with long apical tibial spurs, ca. 3/4 length of basitarsus (these tibial spurs much shorter in the other two species). It is most similar to *H. englundi* with regard to leg MSSC, but the length of the tibial spurs and the denser hairs laterally on the mid tibia should serve to separate the two.

Male (Fig. 1). Body length: 4.8–5.0 mm. Wing length: 4.2 mm. Head. Black; inner eye margins converging just below level of antenna (width ca. width of ocellar tubercle), then diverging slightly to level of upper margin of clypeus; palp and proboscis brown; antenna (Fig. 6) dark brown with arista length subequal to head height.

Thorax (Fig. 1). Mesoscutum, scutellum, and all pleura dark brown; katepisternum and meron with some yellow; dorsocentrals with last pair diverging posteriorly; thoracic setae black: 5 *dc*; 1 *np*; 1+2 *ph*; 1+1 *sa*; 1 *pa*; 1 + 1 *sc*; *ac* absent. Some specimens with 2–4 very tiny hairs anterior to and in line with *dc*.

Legs. C yellow, CII with small spot of dark brown dorsoposteriorly. Femora yellow, brown at extreme apex, apical brown color most evident on mid and hind femora. It4 with large apical spurs ca. 1/3 length of tarsomere; claws large, ca. 1/2 length of It5; otherwise fore leg unmodified and without MSSC. FII (Fig. 8) with 9–10 long stiff black setae ventrolaterally on basal 1/2, a dozen or so shorter, almost peg-like black setae extending further along ventral surface to subapex; ventroapex with 8 small peg-like setae. TII (Fig. 8) almost straight, slightly flared from base to apex; 2 strong black setae on lateral surface near middle; numerous midsized straight setae along ventral mesal surface; apical 1/3 with patch of 9–10 long hairs and a few long fine wavy setae; apical tibial spurs 2/3 length of IIt1. IIt1 2/3 length of IIt2, with thorn like apical spur, IIt2 inserted apically; IIt4 with large apical spurs 1/2 length of tarsomere; claws large, 1/2 length of IIt5, pulvilli small, 1/4 length of claws; otherwise IIt2-5 unmodified. FIII with sparse short spine-like hairs on basal 1/2 of ventral surface; claws large, ca. 1/2 length of IIIt5.

Wing (Fig. 1). Subhyaline throughout; vein M_1 slightly converging with R_{4+5} at wing margin; crossvein m-cu slightly longer than last section of CuA_1; CuAx 0.80; CuA_1 almost reaching wing margin; halter dark brown at extreme base, otherwise bright white.

Abdomen (Fig. 1). Black; stiff black setae posterolaterally on tergite I. Hypopygium light brown; apex of surstyli dark brown; cerci brown.

Female. As in male except as follows: Body all black with blue-green reflections. Pleura with brassy reflections. Wing as in females of *H. hardyi* except CuAx 1.10.

Types. Holotype male (BPBM 16,509) and 3 paratype females from **MARQUESAS**: Hiva Oa: Atuona Valley, Viaoa River, 1040 ft., 30.viii.2001, riffle/pool, 9°47'07.3" S, 139°03'57.0" W, R. Englund. *Other Paratypes*: Hiva Oa: 5 males, 13 females, same locality and date except 1050 ft., swept from wet vertical face next to falls, D.A. Polhemus (USNM); 1 female, same locality and date except collected from pool/cascade, R.A. Englund (BPBM); 1 male, Taaoa Valley, 300–500 ft., 9°29'46" S, 139°04'15" W, rocky stream and waterfall, 24.x.1999, D.A. Polhemus (USNM). Holotype in BPBM. Paratypes in BPBM, USNM, IMLP, and MNHN.

Habitat. Collected from vertical rock surfaces in association with waterfalls (Fig. 5).

Etymology: This species is named for Dan Polhemus, who was one of the expedition participants and who has collected much valuable material of Dolichopodidae from the Marquesas.

Acknowledgments

Ronald Englund and Dan Polhemus collected the material described in this paper. Their fervent interest in and avid pursuit of aquatic Diptera throughout the years with a keen eye to collecting dolichopodids, has kept this author pleasantly occupied. Brad Evans illustrated the map.

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Sex, Flies, and the Genetic Consequence of Small Population Size

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Abstract

Based on results of mate preference studies conducted on Hawaiian *Drosophila* it is suggested that the dynamics of sexual selection play a critical role in genetic differentiation during founder events. The demographic nature of founder populations results in a shift in the distribution of mating types within the population. That is, females that are too choosy in mate selection, under conditions of small population size, may not encounter males that are able to satisfy their courtship requirements. Over a few generations of small population size, strong selection for less choosy females will result in a shift in gene frequencies toward the genotypes of less choosy females. Under these circumstances, the population is now provided with a genetic milieu where previously co-adapted gene complexes become available for recombination. Novel recombinants may be generated which provide the genetic variability required for the founder population to adapt to the new habitat or environment. Thus, the dynamics of sexual selection can be a synergist for species formation.

Introduction

As recently as two decades ago, Mayr (1982) remarked: "Speciation …now appears as the key problem of evolution. It is remarkable how many problems of evolution cannot be fully understood until speciation is understood…" During the ensuing 20 years, there has been renewed interest in understanding the process of speciation. At least two books that address questions of speciation and the evolutionary processes of species formation have been published. Otte & Endler (1989) edited the volume *Speciation and its Consequences* and Lambert & Spencer (1995) published the edited volume *Speciation and the Recognition Concept*. However, it is not the intent of this paper to discuss the various models of speciation and the reader is referred to these two references for a comprehensive review of the topic.

There is little doubt that *adaptation* is the central theme of the evolutionary process and that natural selection results from the interaction between heritable phenotypic variation within populations and the extrinsic environment in which such populations live. In the formulation of his theory of natural selection, Darwin (1859) made the following statement:

> "It may metaphorically be said that natural selection is daily and hourly scrutinizing, throughout the world, the slightest variation; rejecting those that are bad, preserving and adding up all that are good; silently and insensibly working, whenever and wherever opportunity offers, at the improvement of each organic being in relation to its organic and inorganic conditions of life."

Darwin (1859) also proposed the theory of sexual selection to explain the sexually dimorphic characters he observed among a wide diversity of organisms, but suggested that sexual selection was less important than natural selection in bringing about evolutionary change. He stated:

> "Sexual selection depends on the success of certain individuals over others of the same sex, in relation to the propagation of the species; while natural selection depends on the success of both sexes, at all ages, in relation to the general conditions of life. Sexual selection is a struggle between individuals of one sex, generally the males, for the possession of the other sex. The result is not death to the unsuccessful competitor, but few or no offspring…"

Until recently, most biologists accepted the notion that natural selection is the most dominant force in evolutionary processes. Even Darwin acknowledged that "sexual selection will also be dominated by natural selection tending towards the general welfare of the species." He also recognized that the major issue with his sexual selection model is "…in understanding how it is that the males which conquer other males, or those which prove the most attractive to the females, leave a greater number of offspring to inherit their superiority than their beaten and less attractive rivals. Unless this result does follow, the characters which give to certain males an advantage over others could not be perfected and augmented through sexual selection."

Darwin's theory of sexual selection challenged theoreticians to formulate hypotheses for the evolution of female preference for, and the evolution of, secondary sexual traits in males. It may be useful to briefly discuss one of the most notable of these models. The runaway selection model (Fisher, 1930) inferred that the evolution of a sexually dimorphic character in males could result in a correlated response in the female's preference for that character. The model predicted that sexual selection within an interbreeding population would influence female choice and male characteristics to coevolve very rapidly (O'Donald, 1977, 1980; Lande, 1981, 1982; Kirkpatrick, 1982). Furthermore, female preference for a certain male character tends to select for extreme forms of that character until natural selection steps in to maintain the optimum phenotype for that particular environment. The paradox of the runaway selection model is that the opposing forces of sexual selection and natural selection result in reduced genetic variability for such secondary sexual characters in the males. However, without genetic variation, selection can no longer occur; and unless secondary sexual characters either are linked to or are pleiotropic effects of other components of fitness, such conspicuous characters would be energetically and developmentally costly to produce, and individuals possessing such traits would be in greater danger of predation.

In recent years, there has been significant interest in the role of sexual selection and its influence on "the mutual adjustment of the sexes to what may be called the intraspecific sexual environments" (Carson, 1978). The key word in the previous statement is "intraspecific"; sexual selection is indeed an "intraspecific" phenomenon and that while sexual selection can play a very important role in species formation, it is not a "mechanism" by which genetic isolation between daughter populations is selected. Carson (2003) stated that while the Biological Species Concept continues to underlie much of the research in evolutionary biology, he suggested that "…an important consequence of strong mate choice systems is to cast serious doubt on the validity of this theory." He argued that the intraspecific sexual selection system within an interbreeding population "…develops its own complex fitness-associated characters", which are not adversely affected by the occasional hybridization with sympatric or parapatric populations. Over time, the "fitness-associated characters" that arise within a population due to natural as well as sexual selection may confer reproductive barriers that prevent interbreeding with populations within its geographic range. In Carson's view, any genetically-based inter-group isolation that might result from mate choice systems would be wholly incidental side effects and would not represent "selection of genes for isolation".

In this paper, I review a model that describes a possible mechanism by which sexual selection plays an important role in not only maintaining levels of genetic variability especially during small population size, but also in generating new genetic recombinants that provide the basis for selection following population bottlenecks. Based on mate preference studies on Hawaiian *Drosophila* species, it is suggested that sexual selection plays a dominant role, especially during the initial stages of species formation and serve as a possible mechanism for the "genetic reorganization" that accompanies founder event speciation (Carson, 1971; Carson & Templeton, 1984). Also, some previously unpublished data from natural populations of two species of Hawaiian *Drosophila, D. silvestris,* and *D. heteroneura,* provide further evidence of recent and ancient natural hybridization between sympatric populations of these two species, which suggests that two separate founder colonizations led to the evolution of the present day species.

Asymmetrical Mating Preference and Speciation via the Founder Principle

Often, when mate choice experiments between two species or even two populations of the same species are conducted, the outcome is asymmetrical preference. That is, the males of species A may be readily accepted by the females of species B. However, in the reciprocal direction, males of species B are strongly discriminated against by females of species A. While early *Drosophila* researchers observed mating asymmetries in mate preference experiments (e.g., Dobzhansky & Streisinger, 1944; Bastock, 1956; Reed & Reed, 1950; Rendel, 1951), the significance of such asymmetries was not clearly understood. It was often explained by the presence of differential mating propensity or perhaps differences in sexual maturation between the populations. It was not until more recent studies by Kaneshiro (1976, 1980, 1983) that inference was made that the dynamics of sexual selection during small population size provided the mechanism for shifts in the "sexual environment" of the population. It was suggested that during conditions of small population size, there is strong selection for less choosy females in the population since highly discriminating females may never encounter males that are able to satisfy their courtship requirements. Over a few generations of small population size, there would be a shift in the mating distribution of the population towards an increased frequency of less choosy females. Thus, in mate preference experiments between newly derived populations and older more ancient populations, asymmetrical mating preferences were frequently observed. Females from the derived, more recently bottlenecked population mated with males from the ancestral population equally well as males from its own population and often even more so. However, females from the ancestral population, strongly rejected males from the derived population. These observations led to early conclusions that the results of mate preference experiments could be valuable for determining the direction of evolution between pairs of species based on the asymmetrical mating preference (Kaneshiro 1976, 1980, 1983; Kaneshiro & Kurihara, 1981; Arita & Kaneshiro, 1979; Ahearn, 1980; Powell, 1978; Ohta, 1978; Giddings & Templeton, 1983; Dodd & Powell, 1986). Following the initial paper by Kaneshiro (1976) in which it was suggested that mate preference experiments could be useful in predicting the "direction of evolution", a number of other studies (Watanabe & Kawanishi, 1979; Wasserman & Koepfer, 1980; Markow, 1981) that also showed asymmetrical mating preference among *Drosophila* populations concluded that the direction of evolution could well be in the opposite direction as predicted by Kaneshiro's hypothesis.

Three articles published in Volume 21 of the *Evolutionary Biology* series (1987, M. Hecht, B. Wallace & G. Prance, eds.) presented arguments either for or against the Kaneshiro hypothesis. In Ehrman & Wasserman's chapter (Chapter 1) entitled, "The significance of asymmetrical sexual isolation," the authors concluded "The direction of asymmetrical isolation, taken by itself, is an unreliable indicator of direction of evolution." In Chapter 2, DeSalle & Templeton concluded "One of the primary strengths of the Kaneshiro model is that it makes predictions that can be tested both in the laboratory and in the field." The authors also stated "…recent molecular studies confirm the validity of the Kaneshiro model when its assumptions are satisfied and confirm the validity of Ehrman and Wasserman's central thesis that the Kaneshiro predictions are not universally valid." In Chapter 3, Kaneshiro & Giddings concluded "…the generality of the models discussed in the chapters in this volume can only be determined by the rigorous studies of groups other than the endemic Hawaiian drosophilids. The challenge is not just to determine whether mating asymmetries exist within the groups of organisms being studied and whether the direction of evolution predicted by the various asymmetry models points to the correct direction based on other evidence. Rather, we hope that investigators will ask the question of why such asymmetries exist and how they arose."

The Differential Selection Model of Sexual Selection

Based on mate preference experiments on Hawaiian *Drosophila* species and on results of experiments selecting on high and low discrimination among females, Kaneshiro (1989) suggested an explanation for the observed mating asymmetries among related pairs of species in the native drosophilid fauna. The mating experiments indicated that there is a range of mating types segregating among both sexes. That is, among males there are those that are extremely successful at satisfying the courtship requirements of most of the females in the population and indeed these males accomplish most of the matings in the population. There are other males which do very poorly and in fact may not mate at all even if given the opportunity to do so with several receptive females.

Similarly, among females, there are those that those that exhibit higher threshold levels in mating receptivity and strongly discriminate against most of the males in the population. Within the same populations, there are females that have lower receptivity thresholds and will mate with most of the males in the population.

Kaneshiro (1989) suggested that within an interbreeding population, the most likely mating is between the males that are most successful in satisfying the courtship requirements of females and females that are not so choosy in selecting mating partners. The genetic correlation between these two behavioral phenotypes (i.e., highly successful males and less choosy females) is what maintains the range of mating types in the two sexes generation after generation. In this model then, there is differential selection for opposite ends of the mating distribution in the two sexes and therefore, sexual selection itself serves as the stabilizing force in maintaining a balanced polymorphism in the mating system of the population. Such a model would thus avoid the need for natural selection to play a role in maintaining a normal distribution of mating types segregating in the population. The model also avoids the problem of reduced genetic variability that results from the rapid coevolution of female preference for male traits as is described by the runaway selection model.

The results of the selection experiments (described in Kaneshiro, 1989) support the notion that there is a strong genetic correlation between the two behavioral phenotypes in the two sexes. By selecting for choosy females and males with high mating success simultaneously, it was possible to obtain a line whose mating distribution was significantly different from the parent population. Similarly, it was possible to select for the opposite extreme, i.e., less choosy females. By selection for less choosy females and males that are less successful in mating simultaneously, it was possible to obtain progeny whose mating distribution was significantly different from the parent population but in the opposite direction. The data from the selection experiments clearly indicate that there is indeed a range of mating types segregating in both sexes and that there is a strong correlation between female choosiness and male mating ability. By selecting for both of these behavioral phenotypes simultaneously, it was possible to obtain selected lines at both ends of the distribution in as few as two generations of selection.

The Role of Sexual Selection in Founder Event Speciation

Another feature of the differential selection model described by Kaneshiro (1989) is that the sexual selection system is characterized as a frequency dependent system. That is, when the size of the population is significantly reduced, there can be even stronger selection for less choosy females. Under small population size, females that are very choosy may never encounter males that are able to satisfy their courtship requirements. Over a few generations of small population size, there can be a shift in the distribution of mating types in the population until a significant increase in frequency of less choosy females in the population has occurred. Correspondingly, such a shift in mating distribution may be accompanied by a shift in the gene frequencies of the population resulting in the destabilization of the coadapted genetic system that had evolved in the population while adapting to a particular habitat. Such a destabilized genetic environment presents the opportunity for genetic changes conducive to speciation. It is suggested that the breakup of coadapted sets of genes now allows novel genetic recombinants to be generated, some of which may be better adapted to the environmental conditions that led to the reduced population size. Thus, the dynamics of sexual selection in response to significant reduction in population size can play an extremely important role in maintaining levels of genetic variability upon which natural selection can operate in the survival of the population during stress environmental conditions.

In the evolution of island biota such as has been observed in the endemic Drosophilidae of the Hawaiian Islands, it has been suggested that the most likely mode of speciation is what has been referred to as founder event speciation. In most cases, the most probable scenario is that a single fertilized female is blown from one island to an adjacent island where a new colony may be established if suitable habitat and oviposition sites are readily available. During the initial stages of colonization when the population size is small, there would be strong selection for females that are less choosy in mate selection because females that are highly discriminating may never encounter males that are able to satisfy their mating requirements. As suggested in the differential selection model then, within a few generations, there would be a shift in the distribution of mating types in the population toward an increased frequency of less choosy females. There would be a corresponding shift in the gene frequencies of the population followed by a destabilization of the coadapted genetic system. In subsequent generations, novel genetic recombinants may be generated some of which are better adapted to the new habitat. These genotypes are strongly selected, especially if they are linked or correlated with the genotypes of the less choosy females. Clearly, at least during the initial stages of colonization immediately following the founder event, the dynamics of sexual selection may play an important role in producing a genetic environment that is conducive to the formation of new species.

Sexual Selection and Natural Hybridization

In an article on natural hybridization, Arnold (1992) stated:

> “Natural hybridization and introgression…may lead to…the merging of the hybridizing forms…the reinforcement of reproductive barriers through selection for assortative (conspecific) mating…the production of more or less fit introgressed genotypes…[or] to the formation of hybrid species.”

Then in his book entitled “Natural Hybridization and Evolution” published in 1997, Arnold stated:

> “ …the hypothesis addressed in this book is that natural hybridization affects the evolutionary history of the groups in which it occurs primarily through the production of novel genotypes that in turn lead to adaptive evolution and/or production of new lineages. This hypothesis is not new…most recent studies of natural hybridization have, at best, viewed this process as a tool for defining barriers to gene exchange to infer how speciation …might occur. In contrast, I will examine these barriers to facilitate predictions concerning what hybrid genotypes may be produced, because an array of hybrid genotypes represents material for evolution.”

In a paper published by Kaneshiro (1989), it was suggested that under certain conditions, sexual selection as described by the differential selection model actually “permits” natural hybridization between closely related species. Again, a strong frequency-dependent component in the dynamics of the sexual selection system results in an increased frequency of less choosy females over a few generations of small population size. Under these conditions then, the probability that females of the affected population may accept the courtship overtures of males from a related species is greatly increased. Interestingly, many (but certainly not all) of the documented cases of natural hybridization are unidirectional. That is, more often than not, there is evidence of “leakage” of genetic material from one population into another but not vice versa.

Among the Hawaiian *Drosophila*, there are two well-documented cases of natural hybridization: between *D. setosimentum* and *D. ochrobasis* and between *D. silvestris* and *D. heteroneura.* In the case of *D. setosimentum* and *D. ochrobasis* from a particular locality on the Island of Hawai‘i, approximately 2% (4 out of 180) of the individuals were determined to be either F_1 or backcross offspring. Using easily distinguishable markers in the banding sequence of the polytene chromosomes in both species as well as a very distinctive “null” allele in *D. ochrobasis* at the esterase (est-1) locus, Carson *et al*. (1975) were able to determine the parental origin of the hybrids. The data indicated that one of the *D. setosimentum* females collected from the wild population had mated with a *D. ochrobasis* male. However, the other three individuals were determined to be backcross individuals and the direction of the original interspecific matings could not be definitively determined.

Kaneshiro & Val (1977) first reported on the natural hybridization between *D. heteroneura* and *D. silvestris* which are found sympatrically over most of the island of Hawai‘i. From the Kahuku Ranch area near the south end of the island, they found that 1.1% (6 out of 534) of the individuals were of hybrid origin. Here, there are no chromosomal or electrophoretic markers that distinguish the two species. However, there are morphological features that clearly distinguish the two species and a quantitative genetic analysis of these morphological differences (Val, 1977) permitted inferences about the parents of diagnosable hybrid individuals. In Kaneshiro & Val’s (1977) study, only

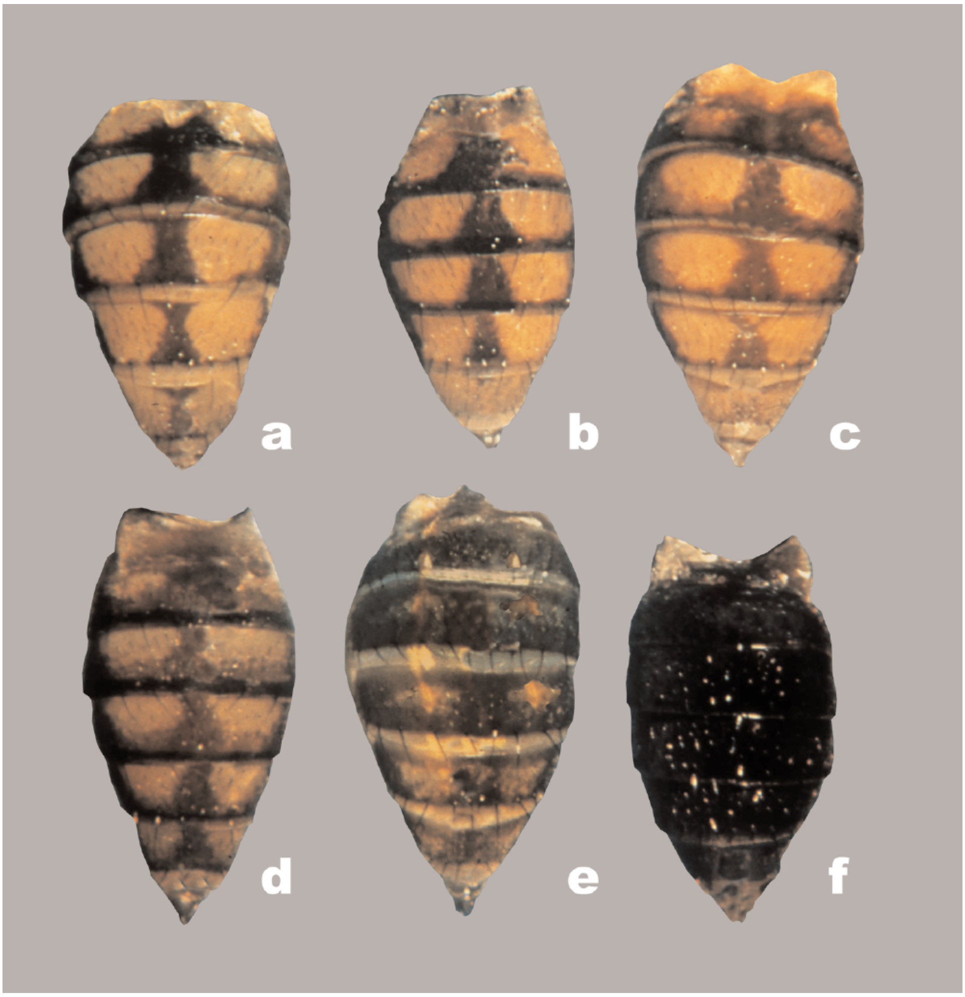

Figure 1. Dorsal view of abdominal patterns of **a.** *Drosophila heteroneura;* **b– e.** *Drosophila silvestris* from various localities on the Island of Hawai‘i where *D. heteroneura* is present; **f.** *D. silvestris* from the Kohala Mts. where *D. heteroneura* is absent.

F_1 hybrid individuals were reported, since determination of F_2 or backcross individuals required metrical analyses. In a subsequent study, Carson *et al*. (1989) conducted the necessary metrical analyses on all wild-caught individuals of both species collected from the Kahuku Ranch area and determined that approximately 1.7% (18 out of 1064) of the individuals were of hybrid origin. Based on the metrical analyses, it was determined that the hybrids were the result of matings between *D. silvestris* females and *D. heteroneura* males, and the backcross individuals appear to be the result of F_1 hybrid (*D. silvestris* females × *D. heteroneura* males) females × *D. silvestris* males. One other hybrid individual between these two species has been collected from a second locality on the island (Carson et al. 1989). This individual was also determined to be a backcross offspring resulting from an F_1 hybrid (*D. silvestris* female × *D. heteroneura* male) female × *D. silvestris* male.

Thus, in all of the documented cases of hybrid individuals between *D. silvestris* and *D. het-*

eroneura, the direction of original interspecific cross is unidirectional, i.e., *D. silvestris* female × *D. heteroneura* male. One other bit of evidence indicates that the leakage of genetic material occurs in the same direction. In the Kohala Mountains in the northern part of the island, where only *D. silvestris* has been found (i.e., *D. heteroneura* is absent there), the abdomen of *D. silvestris* is black in all individuals (Fig. 1f). In all other localities where both species occur sympatrically, the yellow and black abdomen pattern characteristic of *D. heteroneura* (Fig. 1a) appears to be segregating in the *D. silvestris* populations (see Figs. 1a–f). These observations indicate that natural hybridization has occurred between these two species at all localities where they are sympatric (i.e., except in the Kohala Mts where *D. heteroneura* is absent). This evidence indicates that introgression has occurred unidirectionally, again from *D. heteroneura* into *D. silvestris*.

Concluding Remarks

It is suggested that sexual selection is a truly dynamic process that is influenced by density-dependent factors. The differential sexual selection model discussed here may provide an explanation of how genetic variability may be generated even under conditions of small population size over a few generations. Shifts in the distribution of mating types during population bottlenecks result in a genetic environment that is conducive to the generation of novel recombinants. The generation of novel genetic recombinants and the selection for genotypes that are better adapted to changing environmental conditions are enhanced by the sexual selection system especially when the population is subjected to drastic reduction in size. The notion of increased genetic variability during small population size is certainly contrary to classical population genetic models. For example, Mayr (1963), in formulating his founder principle model, emphasized the loss of genetic variability due to genetic drift during the period of reduced population size following the founding of a new colony. Nei *et al.* (1975) concluded that the genetic variability of populations faced with small population size "…is expected to decline rapidly but, as soon as population size becomes large, it starts to increase owing to new mutations." However, there is much evidence that genetic variability may be maintained even when populations are subjected to drastic reduction in size. Fitch & Atchley (1985) reported that old inbred laboratory strains of mice carry large amounts of genetic variability. Carson(1987) reported that a highly inbred stock of *D. silvestris*, which was originally established from a single fertilized female collected from nature, was polymorphic for three inversions in chromosome 4, even after nearly 10 years in the laboratory.

The differential sexual selection model also provides a mechanism by which hybridization between co-existing species is permitted under certain demographic conditions. It is not suggested that introgression is extensive tending toward the destruction of the genetic integrity of the hybridizing species. Rather, it is suggested that there may be "leakage" of genetic material across species barriers that further enhances the population's ability to maintain and even increase levels of genetic variability during reduction in population size.

Clearly, sexual selection models such as the differential selection model provide important insights into mechanisms of species formation, but could also be applied to the development of more effective conservation management programs involving rare and endangered species. Based on the work on the Hawaiian Drosophilidae, it is clear that in most cases, populations that have been subjected to reduction in size due to environmental stress still have the genetic capacity to generate novel genetic recombinants via the differential sexual selection model. Sexual selection should certainly be taken into consideration in captive breeding programs if the goal is to ensure the maintenance of genetic variability. It may also apply to understanding of issues of insecticide resistance which appear to evolve rapidly following treatment. Thus, the demographics of small populations and the genetic consequences of reduced population size as well as the dynamics of the sexual selection system are extremely important aspects of the evolutionary process.

Acknowledgments

This paper is dedicated to the memory of Professor D. Elmo Hardy who served as my mentor during much of my undergraduate and graduate career at the University of Hawaii. October 2003 marks the 40th anniversary since Elmo hired me as a dishwasher on the Hawaiian *Drosophila* Project when I was a second year student at the University of Hawaii. I was a pre-med student at the time but by the time I completed my undergraduate degree I was "hooked" and decided on a graduate program researching the evolutionary biology of the Hawaiian Drosophilidae under Elmo's mentorship. To this day, I continue to investigate the evolutionary processes involved in the explosive speciation of this group and owe much of the success in my career to Elmo's influence and unselfish mentorship during my undergraduate and graduate years at the University of Hawaii.

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Host Alternation by Gall Midges of the Genus *Asphondylia* (Diptera: Cecidomyiidae)[1]

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Abstract

Host alternation by *Asphondylia gennadii* (Marchal) and *Asphondylia baca* Monzen was studied. The DNA analysis revealed that at least *Ceratonia siliqua* Linnaeus (Fabaceae), *Urginea maritime* (Linnaeus) Baker (Liliaceae), and *Capparis spinosa* Linnaeus (Capparidaceae) were included in the host range of *A. gennadii* and that this gall midge can complete its annual life cycle by utilizing these host plants alternatively. The morphological study of pupal frontal area revealed that a gall midge that is responsible for leaf bud galls on *Weigela* species (Caprifoliaceae) in Japan had been misidentified as a North American species, *Asphondylia diervillae* Felt. DNA analysis, together with morphological, ecological, and distributional information, indicated that the weigela leaf bud gall midge is identical with *Asphondylia baca* Monzen that produces fruit galls on *Ampelopsis brevipedunculata* (Maximowicz) Trautvetter var. *heterophylla* (Thunberg) Hara (Vitaceae) and *Cayratia japonica* (Thunberg) Gagnepain (Vitaceae) in Japan. The identity of the two species indicated that *A. baca* exhibits host alternation, using *Ampelopsis* and *Cayratia* fruit for galling in summer-autumn and *Weigela* leaf buds in winter-spring. This is the third finding of host alternation by *Asphondylia* species, suggesting further detections of host alternation in the genus.

Introduction

Host alternation is common to a number of Aphididae and Pemphigidae (Homoptera) but is unusual for other insect groups. In the order Diptera, host alternation has never been reported (A. Freidberg, D. Henshaw, A. Pont, M. Suwa, and M. v. Tschirnhaus, 2002, pers. comm. at the 5th International Congress of Dipterology, Brisbane, Australia) except for 2 gall midge species of the genus *Asphondylia* (Cecidomyiidae) (Harris, 1975; Orphanides, 1975; Yukawa *et al*., 2003).

Asphondylia contains 271 nominal species in the world (Gagné, in press). They are most often responsible for bud, flower, and fruit galls on various plant species. Most of them are monophagous or oligophagous within a single plant genus or family (e.g., Skuhravá, 1986; Gagné & Orphanides, 1992; Gagné, 1994). The annual life cycle of monophagous or oligophagous species can be easily clarified when they are univoltine.

Multivoltine species do not appear to be dominant in *Asphondylia*, but overwintering hosts or spring-summer-autumn hosts still remain unknown for many species. Usually their spring-summer-autumn hosts die back in late autumn and the emergent summer-autumn generation has nowhere to lay their eggs on those hosts. The emergent winter generation has also nowhere to lay its eggs because its winter hosts do not proffer the proper organ for oviposition at the time of adult emergence in spring. Therefore, the multivoltine species require some alternative hosts on which to lay their eggs.

There are 2 known instances of host alternation by *Asphondylia* gall midges. In Cyprus, *Asphondylia gennadii* (Marchal) utilizes carob *Ceratonia siliqua* Linnaeus (Fabaceae) as a winter

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[1] Nucleotide sequence data used in this paper are available in the DDBJ/ EMBL/ GenBank databases under the following accession numbers: AB115562-AB115589, AB086426-AB086428, AB085773-AB085775, AB085777, AB085865, AB085868, AB085874, and AB085877.

host, and many other plants, including pepper *Capsicum annuum* Linnaeus (Solanaceae), caper *Capparis spinosa* Linnaeus (Capparidaceae), and sea squill *Urginea maritime* (Linnaeus) Baker (Liliaceae), as summer hosts (Harris, 1975; Orphanides, 1975; Gagné & Orphanides, 1992). However, host alternation by *A. gennadii* has never been confirmed at the DNA level. In Japan, Yukawa *et al*. (2003) confirmed by DNA analysis that the soybean pod gall midge, *Asphondylia yushimai* Yukawa & Uechi, produces fruit galls on *Prunus zippeliana* Miquel (Rosaceae) in winter and pod galls on soybean *Glycine max* (Linnaeus) Merrill (Fabaceae) or wild fabaceous plants in summer and autumn. On the basis of these examples, Yukawa *et al*. (2003) pointed out that the host alternation might occur elsewhere in the genus *Asphondylia* and that morphologically similar nominal species that utilize different groups of host plant may be synonymized in the future by DNA analysis.

Besides *A. yushimai*, at least 5 nominal species and 14 unidentified segregates of *Asphondylia* have been known to occur in Japan (Yukawa & Masuda, 1996; Yukawa *et al*., 2003). Three species and 1 segregate of them are univoltine and monophagous or oligophagous, but the remainder are multivoltine and part of their life history has been unknown (Yukawa & Masuda, 1996; N. Uechi & J. Yukawa, unpubl. data). Even though these multivoltine species or segregates possibly utilize different groups of host plants, they are morphologically quite similar to each other (Yukawa, 1971; Yukawa & Masuda, 1996).

Sunose (1992) tried to confirm the identity of the ampelopsis fruit gall midge, *Asphondylia baca* Monzen, with the weigela leaf bud gall midge, *Asphondylia* sp., which had been misidentified by Shinji (1938) as a North American species, *Asphondylia diervillae* Felt. Sunose (1992) observed that females of the weigela leaf bud gall midge laid their eggs into fruit of *Ampelopsis brevipedunculata* (Maximowicz) Trautvetter var. *heterophylla* (Thunberg) Hara (Vitaceae) when they were introduced into a small cage covering the fruit. He then suspected that the 2 species might be identical although gall formation was not confirmed on the fruit.

This paper proposes: (1) to reconfirm the host alternation by *A. gennadi* at the DNA level, (2) to revise, by morphological studies, the specific position of the weigela leaf bud gall midge that had been identified as *A. diervillae,* (3) to confirm the identity of the weigela leaf bud gall midge with *A. baca* based on morphological, molecular, ecological, and biogeographical information, and (4) to make remarks about host alternation by *Asphondylia* gall midges.

In order to show clearly the results of the aforementioned purposes, this paper is divided into the following 3 parts: I. *Asphondylia gennadii* from Cyprus; II. *Asphondylia baca* and the weigela leaf bud gall midge in Japan; and III. General remarks.

I. *Asphondylia gennadii* from Cyprus

Material and Methods

Asphondylia gennadii specimens stored in 75% ethanol were sent from Cyprus by Dr. N. Seraphides and Mr. A. Georghiou in March 2003. They consist of 41 pupae from *Ceratonia*, 20 pupae, and 1 larva from *Urginea*, and about 50 pupae from *Capparis*. Unfortunately we could not obtain *A. gennadii* individuals from the following known summer host plants: pepper *C. annuum* (Solanaceae), potato *Solanum tuberosum* Linnaeus (Solanaceae), garden rocket *Eruca vesicaria* Linnaeus (Brassicaceae), mustard *Sinapis* spp. (Brassicaceae), asphodel *Asphodelus fistulosus* Linnaeus (Liliaceae), and St. Johnswort *Hypericum crispum* Linnaeus (Hypericaceae).

Three individuals on *Ceratonia* and 5 on *Urginea* and *Capparis*, respectively, were submitted to DNA analysis. For every individual, total DNA was extracted from the whole body with the Dneasy tissue kit (Qiagen, Japan), following the manufacturer's instructions. A region of the cytochrome oxidase subunit I (COI) gene of mtDNA was amplified, purified, sequenced, and electrophoresized following the methods described by Yukawa *et al*. (2003). This region, together with other regions, has been effectively used for the analysis of intra- or interspecific variations in vari-

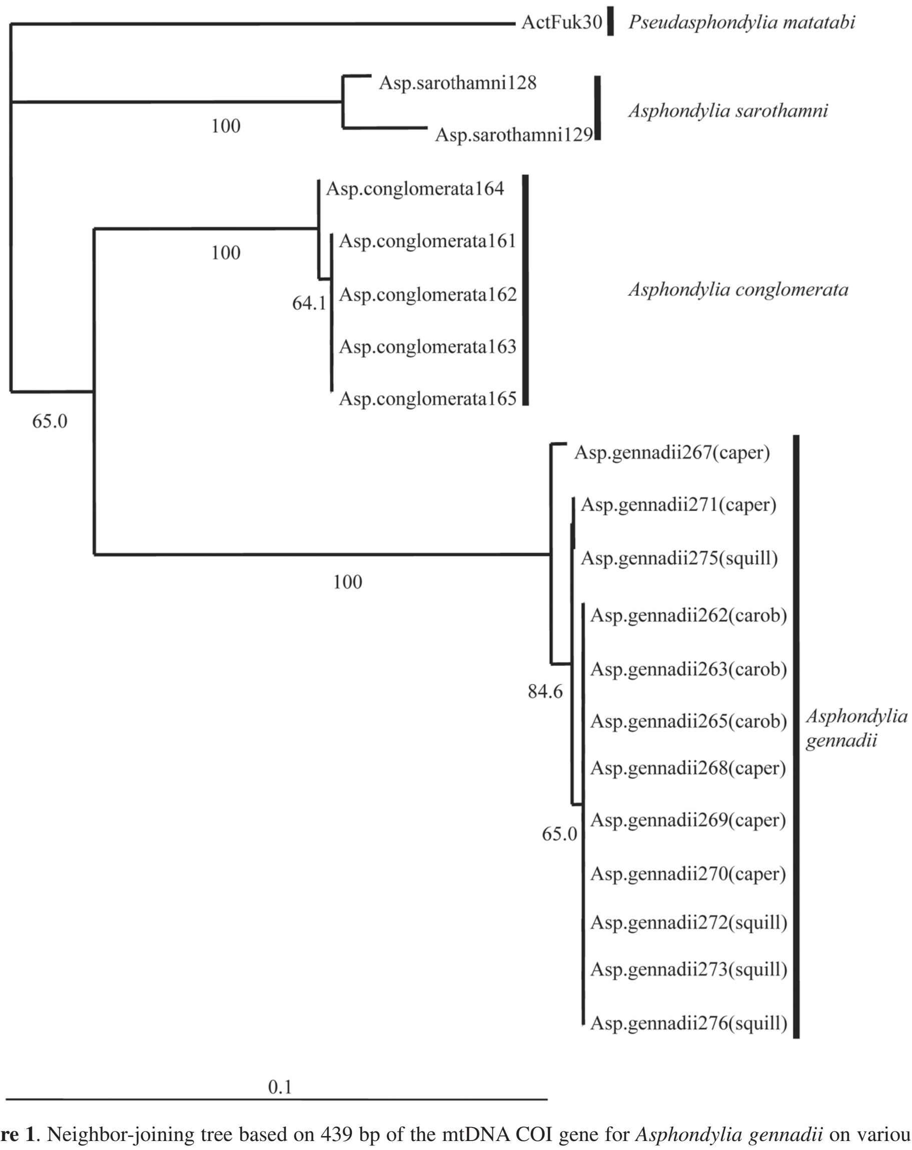

Figure 1. Neighbor-joining tree based on 439 bp of the mtDNA COI gene for *Asphondylia gennadii* on various hosts. Bootstrap values are indicated for nodes gaining more than 60% support (1000 replications). *Pseudasphondylia matatabi*, *A. sarothamni*, and *A. conglomerata* were used as outgroup species. Sample names correspond to the respective isolation names registered in DNA database.

ous insect orders: e.g., Hymenoptera (Scheffer & Grissell, 2003), Heteroptera (Damgaard & Sperling, 2001), Diptera: Cecidomyiidae (Shirota *et al*., 1999; Yukawa *et al*., 2003), Tephritidae (Jamnongluk *et al*., 2003) and Lepidoptera (Andolfatto *et al*., 2003).

The primers used for the amplification were as follows: forward; 5´-GGATCACCTGATATAG-CATTCCC-3´ and reverse; 5´-CCCAAAATTAAAATATAAACTTC-3´. Both strands of the PCR products were sequenced.

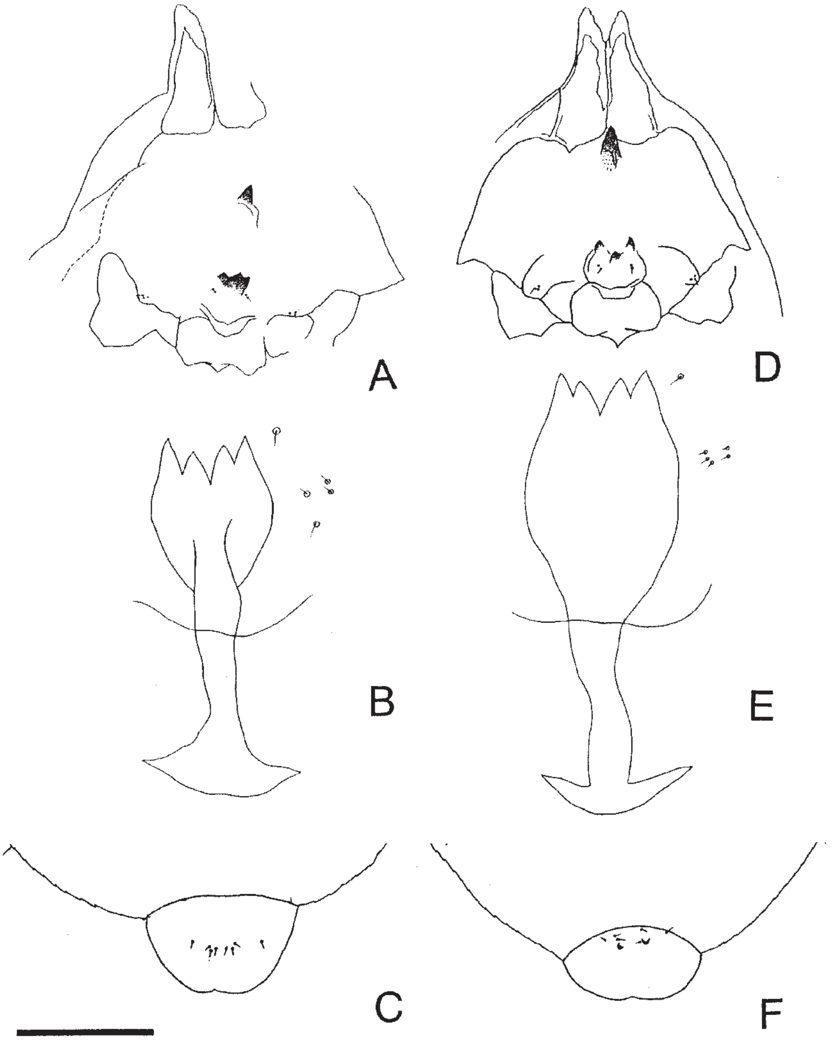

Figure 2. A–C, *Asphondylia diervillae*, **D–F**, the weigela leaf bud gall midge. **A, D**, ventral view of pupal head. **B, E**, larval sternal spatula and adjacent papillae. **C, F**, larval terminal segment and papillae, dorsal view. Scale: 0.8 mm for A, D, 0.2 mm for B, E, and 0.26 mm for C, F.

The sequence data were analyzed by the neighbor-joining (NJ), maximum parsimony (MP), maximum likelihood (ML) methods, and unweighted pair-group method using arithmetic means (UPGMA) with the software package PHYLIP Version 3.573c (Felsenstein, 1993). Evolutionary distances were computed by Kimura's two-parameter distances (Kimura, 1980). The resulting trees were evaluated by the bootstrap test (Efron, 1982; Felsenstein, 1985) based on 1,000 replications for the NJ, MP, and UPGMA trees and 100 replications for the ML tree. The MP, ML, and UPGMA trees are not shown in this paper, since these are quite similar to the NJ tree.

As an outgroup in the above analysis, the following 2 European species of *Asphondylia* and a

Table 1. Gall midges used for DNA analysis

Gall midge	Host plant	English name	Collection site (Collector)	n	Accession No.
Asphondylia gennadii	*Ceratonia siliqua*	carob	Zygi, Cyprus (N. Seraphides & A. Georghiou)	3	AB115569-AB115571
	Capparis spinosa	caper	Ay. Theodovas, Cyprus (N. Seraphides & A. Georghiou)	5	AB115572-AB115576
	Urginea maritime	squill	Mazotos, Cyprus (N. Seraphides & A. Georghiou)	4	AB115577-AB115580
A. conglomerata	*Atriplex halimus* (bud)	tree purslane	Sede Boqer, Israel (N. Dorchin)	5	AB115562-AB115566
A. sarothamni	*Cytisus scoparius*	common broom	Guildford, UK (K. M. Harris)	2	AB115567, AB115568
A. baca	*Ampelopsis brevipedunculata*		Sapporo City, Hokkaido, Japan (N. Uechi)	1	AB115589
			Fukuoka City, Fukuoka Pref., Japan (N. Uechi)	3	AB115581-AB115583
			Hisayama Town, Fukuoka Pref., Japan (N. Uechi)	1	AB115585
			Wakamiya Town, Fukuoka Pref., Japan (N. Uechi)	1	AB115584
			Ume Town, Oita Pref., Japan (J. Yukawa)	1	AB115587
			Kitagawa Town, Miyazaki Pref., Japan (J. Yukawa)	1	AB115588
	Cayratia japonica		Sendai City, Miyagi Pref., Japan (J. Yukawa)	1	AB115586
The weigela leaf bud gall midge	*Weigela hortensis*		See Yukawa *et al.* (2003)	3	AB086426-AB086428
	Weigela coraeensis		See Yukawa *et al.* (2003)	3	AB085773-AB085775
Asphondylia yushimai	*Glycine max*	soybean	See Yukawa *et al.* (2003)	3	AB085777, AB085865, AB085868
The hedera flower bud gall midge	*Hedera rhombea*		See Yukawa *et al.* (2003)	2	AB085874, AB085877
Pseudasphondylia matatabi	*Actinidia polygama*	silver vine	See Yukawa *et al.* (2003)	1	AB085873

Japanese species of *Pseudasphondylia* were used (Table 1): *Asphondylia conglomerata* Stefani galling on *Atriplex halimus* Linnaeus (Chenopodiaceae), *Asphondylia sarothamni* Loew galling on *Cytisus scoparius* (Linnaeus) Link (Fabaceae), and *Pseudasphondylia matatabi* (Yuasa & Kumazawa) (Diptera: Cecidomyiidae), which is responsible for fruit galls on *Actinidia polygama* (Siebold & Zuccarini) Planchon & Maximowicz (Actinidiaceae).

Results

The amplified mitochondrial COI gene fragment was 439 bp long. This region corresponded to the bases 1752–2190 of the genome of *Drosophila yakuba* Burla (Diptera: Drosophilidae) (Clary & Wolstenholme, 1985).

The monophyly of the clade *A. gennadii* on *Ceratonia*, *Capparis*, and *Urginea* was supported by a 100% bootstrap value (Fig. 1). The sequences of *A. gennadii* were distinctly different from those of the 2 European congeners in the outgroup species, *A. conglomerata* and *A. sarothamni* (Fig. 1). There were 51 (11.62% of 439 bp) to 69 bp (15.72%) differences between *A. gennadii* and the 2 species (Table 1) and 6 (4.11%) to 7 (4.80%) differences in the 146 deduced amino acid residues.

Three haplotypes of *A. gennadii* were recognized in this study. However, sequential variations between those on different host plants were very small, 0 (0%) to 4 bp (0.91%) differences, and there were no differences in the 146 deduced amino acid residues.

Discussion

In contrast to the big differences between *A. gennadii* and the outgroup species, intraspecific variations among *A. gennadii* individuals from different host plants are small enough to consider that they are identical species. Thus, the current DNA analysis indicates that at least *Ceratonia, Urginea,* and *Capparis* are included in the host range of *A. gennadii*. As shown in Orphanides (1975), *A. gennadii* can complete its annual life cycle by utilizing these host plants alternatively. This provides the confirmation at the DNA level of host alternation by *A. gennadii*.

Orphanides (1975) mentioned a possible existence of host races or sibling species on summer hosts. They have been temporarily called by common names based on their main summer host plants as the caper midge, the pepper midge, and the squill midge. However, our sequencing data did not indicate the existence of host races or sibling species because there were more than one haplotype on a single summer host and they were not always included in one clade associated with one host species (Fig. 1).

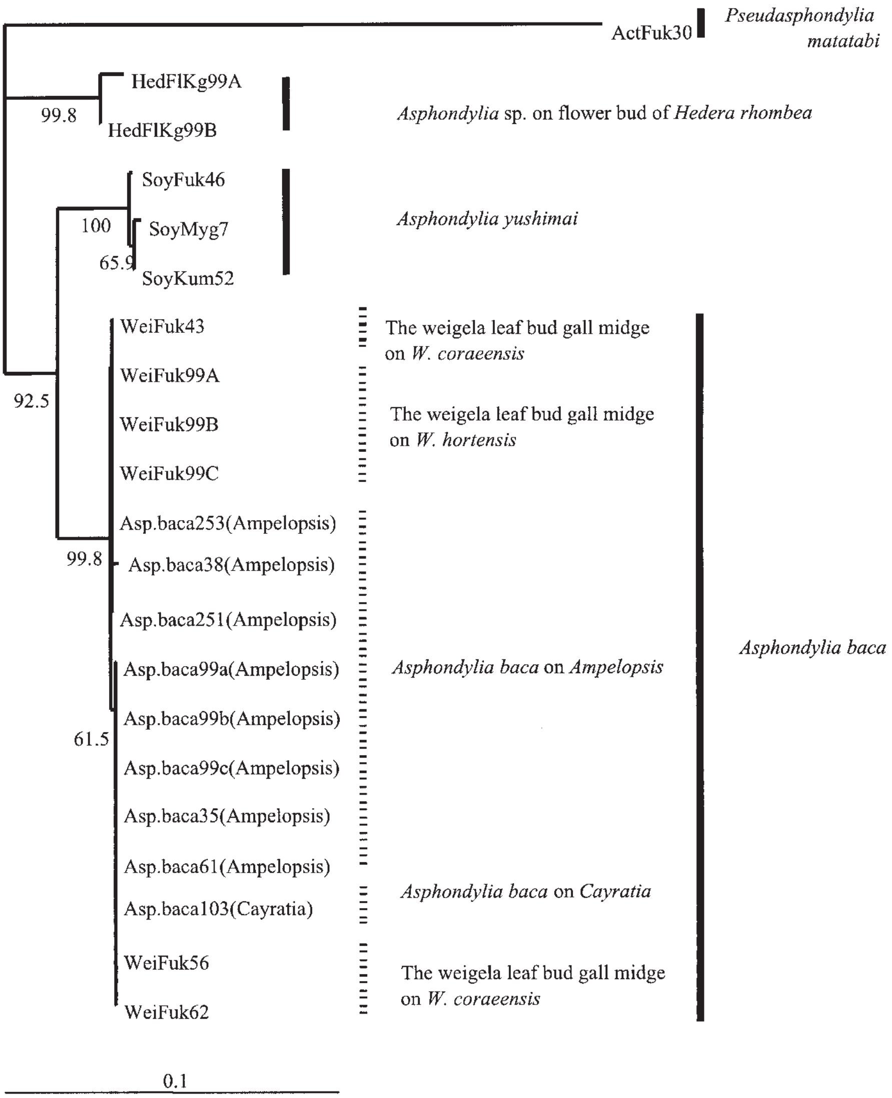

Figure 3. Neighbor-joining tree based on 439 bp of the mtDNA COI gene for *Asphondylia baca* on various hosts, *A. yushimai*, and *Asphondylia* sp. on flower buds of *Hedera rhombea*. Bootstrap values are indicated for nodes gaining more than 60% support (1000 replications). *Pseudasphondylia matatabi* was used as outgroup species. Sample names correspond to the respective isolation names registered in DNA database.

However, with regard to the pepper midge, we require specimens from the Mediterranean for DNA analysis to determine whether or not it is identical with *A. gennadii*, because there were distinct differences in the sequencing data (N. Uechi & J. Yukawa, unpubl. data) between *A. gennadii* and the Indonesian chili pod gall midge that had been identified as *Asphondylia capsici* Barnes (Aunu Rauf, 2001, pers. comm.; see also Skuhravá, 1986 for the occurrence of *A. capsici* in the Oriental Region).

Table 2. ***Asphondylia diervillae*: fronto-clypeal, mesopleural, and mesepimeral setal counts, and measurements of wing, third flagellomere, ovipositor, and female seventh sternite.**

		Male				Female			
		n	mean	s.d.	range	n	mean	s.d.	range
Setal counts	Fronto-clypeal setae	2	37.0	1.4	36-38	2	30.0	7.1	25-35
	Mesopleural setae	1	18.0	-	18	2	38.0	14.1	28-48
	Mesepimeral setae	1	35.0	-	35	2	42.5	5.0	39-46
Wing	Length (μm)	2	3122	332	2887-3357	2	3194	134	3100-3289
	Width (μm)	2	1444	140	1344-1543	2	1511	132	1418-1604
	Length/width	2	2.2	0.02	2.1-2.2	2	2.1	0.1	2.1-2.2
Third flagellomere	Basal enlargement (μm)	2	191.0	26.9	172-210	2	197.0	7.1	192-202
	Width (μm)	2	49.5	13.5	40-59	2	54.5	9.2	48-61
Ovipositor	Length (μm)	-	-	-	-	2	1247.5	36.1	1222-1273
7th sternite	Length (μm)	-	-	-	-	2	318.0	7.1	313-323
	Ovipositor/7th sternite	-	-	-	-	2	3.9	0.2	3.8-4.1

II. *Asphondylia baca* and the weigela leaf bud gall midge in Japan

Material and Methods

Collection and preservation of Japanese Asphondylia *species*

Fruit galls produced by *Asphondylia baca* on *Ampelopsis brevipedunculata* and *Cayratia japonica* (Thunberg) Gagnepain (Vitaceae) and leaf bud galls by *Asphondylia* sp. on *Weigela hortensis* K. Koch and *Weigela coraeensis* Thunberg (Caprifoliaceae) were collected from various localities in Japan (Table 1). In addition to our collecting efforts, many people cooperated in collecting *Asphondylia* galls and gall midges at various localities in Japan. Distribution information was accumulated by literature surveys (Yukawa & Masuda, 1996; Uechi *et al.*, 2002) besides the collecting data of this study.

Some of the collected galls were dissected under a binocular microscope to obtain larval and pupal specimens. Remaining galls were maintained in plastic containers (10 cm in diameter, 6 cm in depth) to rear adult midges. Mature larvae, pupae, or emerged adults were kept in 70 to 75% ethanol for morphological observation or 99.5% acetone for DNA analysis.

The following slide-mounted specimens were examined: 8 males and 8 females, galls collected from Mt. Hikosan, Fukuoka Pref., Japan, 23 May 1965, J. Yukawa leg., emerged on 23 June–3 July 1965, reared by A. Taketani (host plant: *Weigela japonica* Thunberg) Cecid. No. A1601–A1616, A1621; 7 males and 1 female, galls collected from Iino, Miyazaki Pref., Japan, 25 May 1963, J. Yukawa leg., emerged on 9–20 June 1963, reared by J. Yukawa (host plant: *ibid.*), Cecid. No. A1631–A1637, A1640; 5 females, galls collected from Mt. Nyûtô, Akita Pref., Japan, 30 June 1965, J. Yukawa leg., emerged on 3–12 July 1965, reared by J. Yukawa (host plant: *W. hortensis*), Cecid. No. A1656-A1659; 6 males and 5 females, galls collected from Mt. Inunaki, Fukuoka Pref., Japan, 19 June 2000, N. Uechi leg., emerged on 21–23 June 2000, reared by N. Uechi (host plant: *W. coraeensis*), Cecid. No. A1671–A1681. These specimens are kept in the collection of the Entomological Laboratory, Faculty of Agriculture, Kyushu University, Japan.

Morphological Comparison between Asphondylia diervillae *and the weigela leaf bud gall midge in Japan*

In June 2001, one of us, JY, and Dr. R. J. Gagné (Systematic Entomology Laboratory, USDA) visited Albany, NY and the Appalachian Mountains, WV and MD, USA in search of leaf bud galls produced by *Asphondylia diervillae* on *Diervilla lonicera* Miller (Caprifoliaceae) to obtain fresh larvae or pupae for DNA analysis. However, no galls were found on *D. lonicera* in these areas, so DNA could not be analyzed for *A. diervillae*. For morphological comparison between *A. diervillae* and the weigela leaf bud gall midge in Japan, we borrowed 2 males, 2 females, 2 pupae, and 1 larva of *A.*

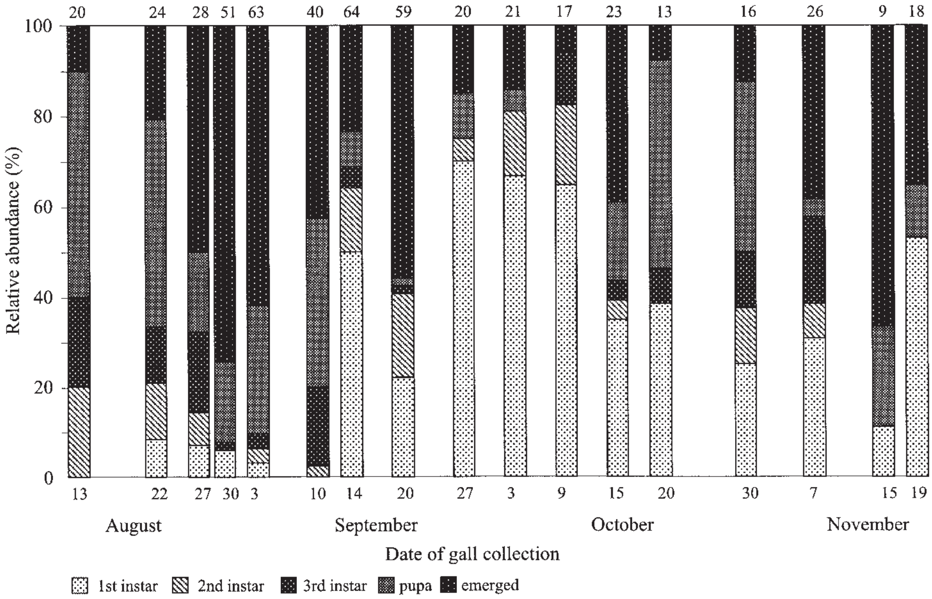

Figure 4. Changes in the age structure of *Asphondylia baca* on *Ampelopsis brevipedunculata* during the period from 13 August to 19 November 1998 at Inunaki, Wakamiya Town, Fukuoka Prefecture, Japan. Numerals above each bar indicate the number of individuals examined.

diervillae from the Felt collection that is presently in the Department of Entomology, Smithsonian Institution, Washington, D.C. Their collection data are as follows (Reference No. a1469 for all the specimens): 1 male, Albany, 29 May 1907; 1 male and 1 pupa, Albany, 17 Aug. 1907; 1 female, Albany, 22 May 1907; 1 female, Albany, 12 Aug. 1907; 1 pupa, Albany, 24 May 1907; 1 larva, Albany, 12 May 1907.

Comparison in the DNA sequencing data and morphological features between Asphondylia baca *and the weigela leaf bud gall midge in Japan*

In order to confirm the identity between *Asphondylia baca* and the weigela leaf bud gall midge, a partial COI region of mtDNA was analyzed by the aforementioned methods applied to *A. gennadii* from Cyprus. Eight individuals of *A. baca* on *Ampelopsis* and 1 on *Cayratia* were submitted to the analysis (Table 1). DNA sequence data for 3 individuals of the weigela leaf bud gall midge on *W. hortensis* and 3 on *W. coraeensis* were available from Yukawa *et al.* (2003) (Table 1). For comparison with *A. baca* and the weigela leaf bud gall midge, we used DNA sequence data for the following Japanese species and segregate that were available from Yukawa *et al.* (2003): *A. yushimai*, *Asphondylia* sp. on flower bud of *Hedera rhombea* (Miquel) Bean (Araliaceae), and *P. matatabi* (Table 1).

Morphological similarity between *A. baca* and the weigela leaf bud gall midge was confirmed by examining the slide-mounted specimens of *A. baca* used in Yukawa (1971). In addition, we examined at least 20 of ethanol-stored larval specimens of *A. baca* to confirm whether or not the shape of apical lobe of sternal spatula is consistent in the species. The larvae were collected by one of us, NU, in July to August 1998 from fruit galls produced on *A. brevipedunculata* at Mt. Inunaki and Mt. Hikosan, Fukuoka Prefecture, Japan.

Table 3. The weigela leaf bud gall midge: fronto-clypeal, mesopleural, and mesepimeral setal counts, and measurements of wing, third flagellomere, ovipositor, and female seventh sternite

		Male				Female			
		n	mean	s.d.	range	n	mean	s.d.	range
Setal counts	Fronto-clypeal setae	4	40.3	12.2	22-48	7	35.7	10.3	25-52
	Mesopleural setae	12	34.3	14.5	13-52	9	45.1	5.1	36-52
	Mesepimeral setae	14	42.1	7.4	28-51	12	45.8	11.0	22-58
Wing	Length (μm)	8	3532	219	3188-3813	8	3867	408	2938-4250
	Width (μm)	8	1367	108	1250-1563	8	1625	88	1438-1688
	Length/width	8	2.6	0.2	2.2-2.7	8	2.4	0.3	1.7-2.8
Third flagellomere	Basal enlargement (μm)	14	253.2	33.0	200-305	14	216.1	25.4	170-250
	Width (μm)	14	59.3	10.5	45-80	14	51.1	12.0	35-75
Ovipositor	Length (μm)	-	-	-	-	6	1378.8	29.8	1333-1424
7th sternite	Length (μm)	-	-	-	-	6	382.2	28.1	343-414
	Ovipositor/7th sternite	-	-	-	-	6	3.6	0.3	3.2-4.1

Changes in the age structure of Asphondylia baca

Ten trees of *Ampelopsis brevipedunculata* were established as census trees at Inunaki, Wakamiya Town, Fukuoka Prefecture, Japan. From August to November 1998, 30–150 fruit galls produced by *A. baca* were collected by two of us, NU and DY, from these trees, 3–5 times a month. They were measured (diameter, height) and dissected to record developmental stages of the gall midge.

Adult emergence season of the weigela leaf bud gall midge

To monitor adult emergences of the weigela leaf bud gall midge, a total of 48 twigs of *W. hortensis* were numbered on 5 May 2000 with plastic labels at Nagatani Dam Park, Fukuoka City, Fukuoka Prefecture, Japan. There were at least 140 bud galls on these twigs. The number of adult emergences was recorded in the field every other day. After recording the number, pupal cases left on the galls were removed and emergence holes were marked with a felt pen to avoid double counting.

Results

Morphological comparison between Asphondylia diervillae *in North America and the weigela leaf bud gall midge in Japan*

Adults were morphologically quite similar to each other. There were no distinct differences between *Asphondylia diervillae* and the weigela leaf bud gall midge in the setal counts and the measurements of wing and third flagellomere (Tables 2, 3). The measurements of ovipositor and seventh sternite were a little shorter in *A. diervillae* than in the weigela leaf bud gall midge, but there were no differences between them in the relative length of ovipositor to the seventh sternite.

In contrast to the adult morphology, the arrangement of 3 lobes of lower frontal horn of pupa clearly indicated that they are different species. The lobes are arranged in a row in *A. diervillae* (Fig. 2A), while the central lobe is located posterior to the 2 outer lobes in the weigela leaf bud gall midge (Fig. 2D). Such a nonlinear arrangement of lobes of lower frontal horn is common in Japanese *Asphondylia* gall midges (Yukawa, 1971; Yukawa & Miyamoto, 1979). In addition, the total number of inner and outer lateral papillae of all larval thoracic segments is 4 in *A. diervillae* (Fig. 2B), while 5 in the weigela leaf bud gall midge (Fig. 2E). All 6 terminal papillae have a short seta, respectively, in the larva of *A. diervillae* (Fig. 2C). In contrast, 2 of 6 terminal papillae are cone-shaped and each of remaining 4 papillae has a short seta in the larva of the weigela leaf bud gall midge (Fig. 2F).

Based on these differences, we considered that the weigela leaf bud gall midge in Japan is not identical with *A. diervillae* in North America.

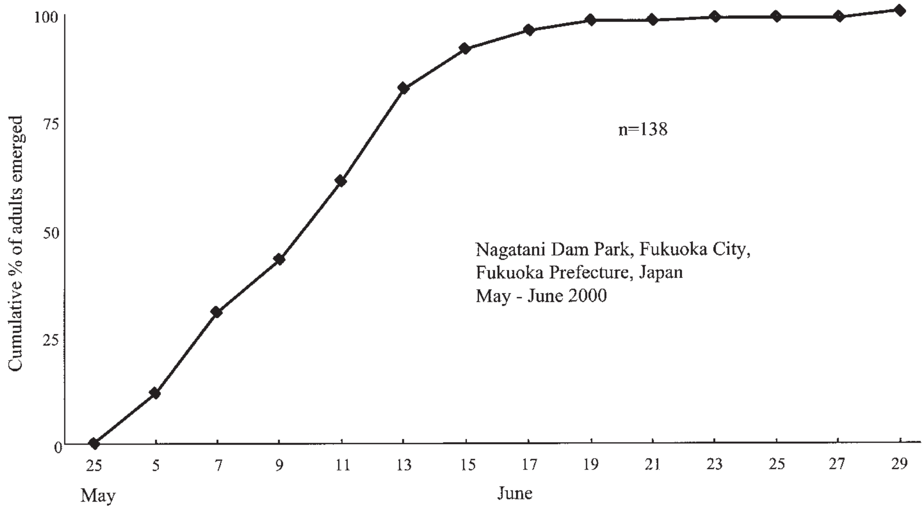

Figure 5. Cumulative percentage emergence curve for the weigela leaf bud gall midge.

Comparison in the DNA sequencing data and morphological features between Asphondylia baca *and the weigela leaf bud gall midge in Japan*

Three haplotypes were recognized in *Asphondylia baca* on *Ampelopsis* (Fig. 3), and there were only 1 to 2 bp differences among them. The sequence data of an individual on *Cayratia* coincided with 1 of the 3 haplotypes of *A. baca* on *Ampelopsis* (Fig. 3). In the weigela leaf bud gall midge, there were 2 haplotypes (Fig. 3), which were only 1 bp different from one another. One of the haplotypes of the weigela leaf bud gall midge was identical with 1 of the 3 haplotypes of *A. baca* on *Ampelopsis* (Fig. 3). All 146 deduced amino acid residues were identical between *A. baca* and the weigela leaf bud gall midge. Monophyly of the clade including the weigela leaf bud gall midge and *A. baca* on *Ampelopsis* and *Cayratia* was supported by a high bootstrap value (Fig. 3).

We examined the redescriptions of *A. baca* and the weigela leaf bud gall midge in Yukawa (1971), and could not find any features to distinguish them except the shape of apical lobe of sternal spatula. However, we confirmed by the observation of further larval specimens that there were individual variations in the apical lobe of sternal spatula from pointed to slightly rounded shape.

Changes in the age structure of Asphondylia baca

On 13 August 1998, all of the developmental stages except 1st instar were found in the galls on *Ampelopsis brevipedunculata* (Fig. 4). Thereafter the relative abundance of adults emerged to other stages increased and reached 75% on 30 August and numbers of adults continued to emerge until late September. In early October, the relative abundance of 1st instars increased, and then a small peak of adult emergence appeared in mid October. From late October to mid November, the rate of adults emerged increased again (Fig. 4). These data indicated that *A. baca* had at least 3 generations on *Ampelopsis* during the period from August to November. In late November, a considerable number of galls contained first instars, but these galls decayed or dropped to the ground in December before the larvae became full-grown.

Adult emergence of the weigela leaf bud gall midge

A total of 138 adults were recognized to have emerged from 116 galls out of about 140 that had been monitored in the field. The remaining 24 galls decayed or withered before emergence. The emergence started on 25 May 2000 and continued until 29 June 2000 (Fig. 5). The percentage of accumulated emergences reached 50% on 11 June, 3 weeks after starting of emergence.

Distributional information

Galls of both *Asphondylia baca* and the weigela leaf bud gall midge have been recorded from various localities in Japan (Yukawa & Masuda, 1996; Uechi *et al*., 2002). In the present study, we newly found these galls in the following places: Mt. Tarumaesan, Hokkaido on *Weigela middendorffiana* (Carriére) K. Koch (Japanese name: Ukon-utsugi) (new host record); Futo, Ito City, Shizuoka Prefecture on *W. coraeensis*; Mt. Azumasan, Hiroshima Prefecture on *W. hortensis*. These collection records indicate that the distribution range of both *Asphondylia baca* and the weigela leaf bud gall midge widely overlap in Japan.

Discussion

Species identification of the weigela leaf bud gall midge

Shinji (1938) identified the host plant of the weigela leaf bud gall midge in Japan as *Diervilla japonica* Candolle (Caprifoliaceae), instead of *W. hortensis*. Based on the similarity of host plant, he believed that the gall midge is identical with a North American species, *A. diervillae*, which produces bud galls on *D. lonicera*. Yukawa (1971) and Yukawa & Masuda (1996) tentatively followed Shinji's identification, because the larval and pupal stages of the Japanese specimens were not precisely compared with those of *A. diervillae* at that time.

However, we found clear morphological differences between *A. diervillae* and the weigela leaf bud gall midge in Japan by comparing the Felt's specimens from North America with Japanese specimens (Fig. 2). This result is quite natural, because there is little possibility that North American and Eurasian (including Japanese) gall midge species are identical, although many genera are common on the 2 continents (Gagné, 1989). This shows that species identification based only on gall resemblance and host plant information can lead to misidentification.

Now that the weigela leaf bud gall midge and *A. diervillae* are shown to be distinct species, the next step is a comparison between the weigela leaf bud gall midge and *A. baca* to confirm their identity suspected by Sunose (1992).

Comparison in the DNA sequencing data and morphological features between Asphondylia baca *and the weigela leaf bud gall midge in Japan*

An *Asphondylia* segregate inhabiting fruit galls on *Cayratia japonica* was identical with *A. baca* in sequencing data (Fig. 3) and morphological features, so we recognized *A. brevipedunculata* and *C. japonica*, both Vitaceae, as summer-autumn host plants of *A. baca*.

We confirmed by our DNA analysis that at least 2 species of the genus *Weigela*, *W. hortensis* and *W. coraeensis*, are winter hosts of the weigela leaf bud gall midge (Fig. 3). These results suggest that other *Weigela* species, *W. middendorffiana*, *W. japonica*, and *Weigela decora* (Nakai) Nakai, are possibly included in the winter host plant range of the gall midge, although the DNA of *Asphondylia* gall midges reared from leaf bud galls on these plants could not be analyzed.

Since at least 1 haplotype of the weigela leaf bud gall midge coincided with 1 of the haplotypes of *A. baca* (Fig. 3) and there were no differences in all 146 deduced amino acid residues between them, we confirmed that the weigela leaf bud gall midge is identical with the ampelopsis fruit gall midge, *A. baca*.

In addition, there were no morphological differences between *A. baca* and the weigela leaf bud gall midge. The only morphological difference, the shape of apical lobe of larval sternal spatula (Yukawa, 1971), was shown to be insignificant in distinguishing the segregates. Thus, the field observation by Sunose (1992) was supported both by the DNA analysis and by the morphological study.

The DNA sequences of the weigela leaf bud gall midge (now identified as *A. baca*) are quite different from those of *A. yushimai* (Fig. 3) and many other *Asphondylia* segregates in Japan

(Yukawa *et al*., 2003; N. Uechi & J. Yukawa, unpubl. data). This means that *A. baca* is a distinct species and does not use known host plants of other *Asphondylia* species or segregates in Japan.

Life history of Asphondylia baca

On the basis of the aforementioned results, we consider that *Asphondylia baca* exhibits host alternation, utilizing *A. brevipedunculata* and *Cayratia japonica* as summer-autumn hosts and *Weigela* species as winter-spring hosts. Although *Ampelopsis* or *Cayratia* fruit do not exist from winter to spring, *Weigela* overwintering leaf buds are available for the gall midge. *Asphondylia baca* can overwinter inside *Weigela* overwintering leaf buds as first instars. Adults of *A. baca* emerge in June from *Weigela* leaf bud galls. Most of them leave *Weigela* and lay their eggs into young fruit of *Ampelopsis* or *Cayratia*. The infested young fruit grow into galls, in which the larvae mature and pupate. After spending 2 or more generations on summer-autumn hosts, adults of *A. baca* emerge in middle to late autumn, but there are no young fruit on *Ampelopsis* and *Cayratia* available for them to oviposit in this season. Instead, they lay their eggs in the overwintering buds of *Weigela* species.

III. General remarks

The example of host alternation by *Asphondylia baca* is the third finding in an *Asphondylia* species, following *A. gennadi* (Orphanides, 1975) and *A. yushimai* (Yukawa *et al*., 2003). The current findings, together with the preceding instances, indicate that host alternation may occur elsewhere in multivoltine species of the genus *Asphondylia* and that morphologically similar nominal species that utilize different groups of host plants may be found to be synonymous through DNA analysis.

It is too premature to remark on the evolution of host alternation by gall midges because information available for discussion is limited. However, we can naturally suspect that the host alternation has ecological significance such as an increase of voltinism that enhances reproductive potential, escape from parasitoid attacks by changing habitats, seeking for more fresh and nutritive host as has been noted for aphids.

Host alternation could evolve in groups of gall midges with strong flight ability. For example, the flight ability of the soybean pod gall midge, *Asphondylia yushimai*, is known to be strong enough to search for the winter hosts away from the summer hosts and *vice versa* (Yukawa *et al*., 2003).

The galls of *Asphondylia* species are always accompanied by a fungal symbiont (Gagné, 1989). There are various papers (e.g., Bronner, 1992; Richter-Vollert, 1964; Rohfritsch, 1992) suggesting, *in vitro* or indirectly, that larvae of ambrosia gall midges take nutritive substances not only from their host plants but also from associated fungi. Since we do not know enough about the role of the fungus, we need further studies to examine whether or not the fungal association has allowed *Asphondylia* species to utilize plant species across different plant families.

Acknowledgments

We are very grateful to Dr. R. J. Gagné (Systematic Entomology Laboratory, USDA) for his critical reading of an early draft, loan of the specimens of *A. diervillae*, and help in the field survey. We wish to express our thanks to Dr. K. M. Harris (former Director of the International Institute of Entomology), Dr. N. Dorchin (Tel Aviv University), Dr. G. M. Orphanides, Dr. N. Seraphides, and Mr. A. Georghiou (Agricultural Research Institute, Cyprus) for providing us with specimens of some *Asphondylia* species for DNA analysis. Our thanks are due to Mr. H. Kikuchi (Hokkaido, Japan), Dr. and Mrs. K. Kiritani (Shizuoka Prefecture, Japan), and Mr. F. Kodoi (Kyushu University) for distributional information on *A. baca* on *Weigela* species. We also thank Dr. T. McCabe (New York State Museum) for his help in the field survey near Albany, NY, USA. This study was supported in part by a research fund to JY from the Yamazaki Spice Incorporated Foundation and is contributed from the Entomological Laboratory, Faculty of Agriculture, Kyushu University, Fukuoka, Japan (Ser. 5, No. 101).

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D. Elmo Hardy Memorial Volume. Contributions to the Systematics and Evolution of Diptera. Edited by N.L. Evenhuis & K.Y. Kaneshiro.
Bishop Museum Bulletin in Entomology 12: 67–77 (2004).

New Species and New Records of Tephritidae (Diptera) from New Caledonia

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Abstract

Tephritidae collected from New Caledonia by M.E. Irwin, E.I. Schlinger, and D.W. Webb were studied and identified. The 18 species represented include 3 new species, *Austronevra irwini*, *Ceratitella schlingeri*, and *Euphranta hardyi*, and 6 species reported from New Caledonia for the first time. The total number of Tephritidae from the island is increased from 16 to 25.

Introduction

D. Elmo Hardy was one of the most prolific taxonomists to study the family Tephritidae. He proposed more than 460 tephritid species names, second only to E.M. Hering in this regard, and he named the most valid species (Norrbom *et al*., 1999a). His large monographic works and cataloging efforts on the Oriental and Australasian faunas have paved the way for continued progress by his successors. Therefore we are honored to dedicate this paper to his memory.

The fruit fly (Diptera: Tephritidae) fauna of New Caledonia is poorly known. Only 15 species were recorded by Norrbom et al. (1999b), 11 belonging to the genus *Bactrocera*. *Euphranta lemniscata* (Enderlein) was also recently recorded by Hancock & Drew (2003). Thanks to the efforts of M.E. Irwin, E.I. Schlinger, and D.W. Webb, we examined a small but interesting collection of tephritids from the island, mainly collected by Malaise traps. We also examined a few additional specimens from the Queensland Museum. Of the 18 species we examined, 3 are described as new species and 6 others are new records for New Caledonia, increasing the total number of tephritid species now known from the island to 25. Additional collecting focused on fruit flies will undoubtedly increase this number. The examined specimens are deposited in the collections of the Illinois Natural History Survey (INHS), the Museum National d'Histoire Naturelle, Paris (MNHN) (the depository for the holotypes of the new species), the National Museum of Natural History, Smithsonian Institution (USNM), or the Queensland Museum (QM).

Tephritidae from New Caledonia

Tephritidae previously recorded from New Caledonia but not present in the examined material include: *Bactrocera curvipennis* (Froggatt), *B. grandistylus* Drew & Hancock, *B. mucronis* (Drew), *B. paraxanthodes* Drew & Hancock, *B. perpusilla* (Drew), *B. tryoni* (Froggatt), and *Dacus aneuvittatus* Drew. Except for the new species, the species listed below were previously known from New Caledonia unless otherwise indicated.

Anastrephoides sp.

Comments. This new species is being described by Ho-Yeon Han (in prep.). This genus was previously known only from the eastern Palaearctic Region.

Austronevra irwini Norrbom & Hancock, **new species**
(Fig. 1A)

Diagnosis. This species belongs in *Austronevra* based on its long oviscape and similarity with the previously known species (from Australia) in chaetotaxy (except for lacking medial scutellar seta), thorax color, and wing pattern. It keys to *Micronevrina* in Permkam & Hancock (1995), but the female terminalia are longer and the aculeus is simple. The arista also is haired only dorsally as in *Austronevra bimaculata*. *Austronevra irwini* differs from the other species of *Austronevra* in having no distal hyaline mark in cell r1 and only 2 pairs of scutellar setae. *Dirioxa*, *Lumirioxa*, and some *Termitorioxa* species are also similar in wing pattern and arista vestiture, but they lack subapical hyaline spots in cells r2+3 and r4+5 and have 3 pairs of scutellar setae.

Description. Body 6 mm long, mostly yellow to orange. Wing 5.8 mm long, 2.3 mm wide. Mesonotum 1.98–2.28 mm long. Setae dark brown.

Head. Entirely yellow to orange except brown ocellar tubercle and paler brown, sometimes diffusely margined spots on medial occipital sclerite and dorsally on lateral occipital sclerite. Frons with 1–2 frontal setae near anterior margin and 2 well-developed orbital setae; ocellar seta weak, slightly longer than ocellar tubercle; postocellar setae well developed. Genal height ca. 1/3 longest diameter of eye. First flagellomere orange brown to brown, ca. 2 × as long as wide. Arista plumose, with dorsal hairs long and in 2 diverging rows, ventrally bare or at most with 3 small hairs.

Thorax. Mostly orange. Mesonotum with dark brown lateral vitta from anterior margin along margins of postpronotal lobe and scutum, across notopleuron, to slightly beyond transverse suture. Posterior margin of scutum, between acrostichal and dorsocentral lines, with moderate brown, diffuse spots. Extreme basoventral corner of side of scutellum, most or all of anatergite and lateral third of mediotergite also dark brown. Extreme apex of scutellum yellow. Thorax entirely evenly microtrichose. Scutellum without setulae. Following setae well developed: postpronotal, 2 notopleural, presutural supra-alar, postsutural supra-alar, intra-alar, postalar, dorsocentral (aligned midway between postsutural supra-alar and intra-alar setae or slightly closer to the latter), acrostichal, basal and apical scutellar, 1–2 anepisternal, and katepisternal; anepimeral seta undifferentiated from setulae; intra-postalar and medial scutellar setae absent.

Legs. Entirely yellow. Ventral setae of femora slender, not spinelike. Mid tibia with 1 ventroapical spinelike seta.

Wing (Fig. 1A). Mostly brown with following hyaline areas: anteromedial spot in cell bc; middle half of cell c and slightly narrower area in cell r1 posterior to it; large, subquadrate spot extending across cell br in distal half; large marginal triangular mark at apex of vein R_1, extending to or almost to vein R_{4+5}, its apex distal to R-M; small ovoid isolated subapical spot in cell r2+3; large ovoid spot anterior to DM-Cu and small ovoid isolated subapical spot in cell r4+5; large isolated ovoid spot in cell m; large ovoid subapical spot in cell dm; small spot in middle of cell cu1 bordering vein Cu1; and main part of cell bcu except extreme base and apex. Remainder of cell bc and area posterior to it in cell br, alula, anal lobe, and most of posterior half of cell cu1 faint brown to subhyaline. Cell bm and posterobasal third of cell dm pale brown. Vein R_{4+5} densely setulose dorsally almost to apex. Veins M, Cu, and Cu_1 nonsetulose.

Abdomen. Yellow medially. Syntergite 1+2 yellow except narrow dark brown lateral margin on distal 2/3. Other tergites with lateral 1/4–1/3 dark brown.

Female terminalia. Oviscape entirely dark brown, cylindrical, 1.75–1.81 mm long, longer than preabdomen, 0.80–0.92 × as long as mesonotum; apically with small medial indentation instead of lobe. Aculeus tip simple, with distinct basal and medial sutures, and 2 pairs of large setulae, almost as long as width of tip. Three spermathecae, spherical, with slender sclerotized neck.

Type Specimens. Holotype ♂ (Museum National d'Histoire Naturelle, Paris; USNM00214887), **NEW CALEDONIA**: Mt. Pinae Trail, 200m, MT, 11–25 Nov 1992, E. & M. Schlinger & D.W. Webb. Paratypes: **NEW CALEDONIA**: Mt. Khogis, 17 km NNE Nouméa, 500 m, 24–26 Dec 1991, M.E. Irwin & D.W. Webb, Malaise trap across forest stream, 1♀ (INHS; USNM00214886). Mt. Pinae Trail, 200 m, MT, 11–25 Nov 1992, E. & M. Schlinger & D.W. Webb, 1♀ (USNM; USNM00214888).

Etymology. This species is named for Mike Irwin, one of the collectors of the type series.

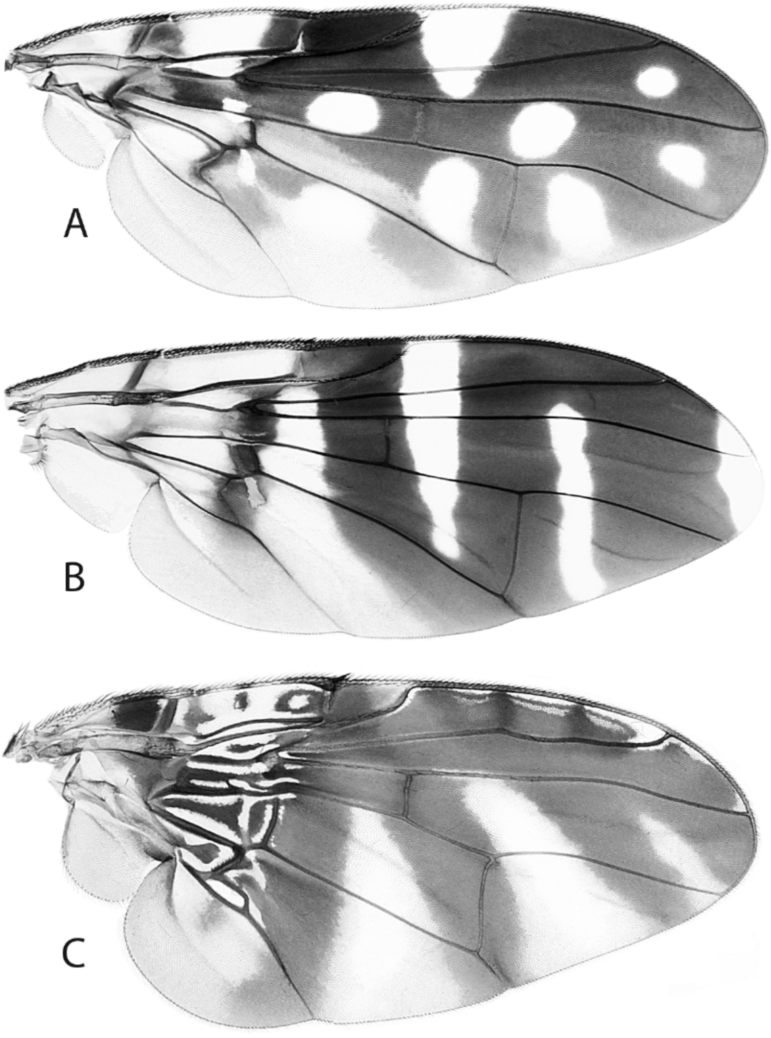

Figure 1. Wings. **A**. *Austronevra irwini*; **B.** *Ceratitella schlingeri*; **C**. *Euphranta hardyi*.

Bactrocera caledoniensis Drew

Bactrocera caledoniensis Drew, 1989: 76.

Specimens Examined. NEW CALEDONIA : Prov. Sud, 9.1 km NW Sarraméa, 21°35'07"S 165°47'24"E, 425 m, Malaise trap on forested hillside, 14 Jan 1996, M.E. Irwin, D.W. Webb & E.I. Schlinger, 1♂ (USNM; USNM00214154).

Bactrocera ebenea (Drew)

Dacus ebeneus Drew, 1971: 65.

Specimens Examined. NEW CALEDONIA : Rivière Bleue Prov. Pk., 213 m, Malaise trap across forest path, 19–20 Nov 1992, D.W. Webb & E. & M. Schlinger, 1♂ (INHS; USNM00214163).

Bactrocera fulvifacies (Perkins)

Zeugodacus fulvifacies Perkins, 1939: 32.

Specimens Examined. NEW CALEDONIA: Rivière Bleue Prov. Pk. 28 km N Yaté, Malaise trap across running stream, 23–27 Dec 1991, M.E. Irwin & D.W. Webb, 1♀ (INHS; USNM00214155). Rivière Bleue Prov. Pk., km 21.9 Riv. Bleue road, Malaise trap in Maquis de Crête, 30 Oct–3 Nov 1992, 320 m, M.E. Irwin, D.W. Webb, E. & M. Schlinger, 1♀ (USNM; USNM00214160). Lucky Creek, 0.5 km N Plum, 19 Dec 1991, D.W. Webb, 1♂ (USNM; USNM00214159). North side of Mont. Dore 4 km NW Plum, Malaise trap in dry wash, 24–27 Dec 1991, M.E. Irwin & D.W. Webb, 1♂ 2♀ (INHS; USNM00214156–58).

Bactrocera psidii (Froggatt)

*Tephritis psidi*i Froggatt, 1899: 500.

Specimens Examined. NEW CALEDONIA: Prov. Sud, Mt. Khogis, 17 km NE Nouméa, 22°10'34"S 166°30'17"E, 425 m, Malaise trap across path in rainforest, 29 Jan 1996, M.E. Irwin D.W. Webb & E.I. Schlinger, 1♀ (INHS; USNM00214143).

Bactrocera umbrosa (Fabricius)

Dacus umbrosus Fabricius, 1805: 274.

Specimens Examined. NEW CALEDONIA : Prov. Sud, 1 km N Sarraméa, 21°38'14"S, 165°51'35"E, Malaise trap on forest hillside, 10 Jan 1996 M.E. Irwin, D.W. Webb & E.I. Schlinger, 1♂ 1♀ (INHS; USNM00214161-62).

Ceratitella schlingeri Norrbom & Hancock, **new species**
(Figs. 1B, 2A–E)

Diagnosis. This species is similar to *C. bifasciata* Hardy, *C. recondita* Permkam & Hancock, and *C. solomonensis* Hancock & Drew, but differs from all 3 species in the color of the postpronotal lobe (brown surrounding postpronotal seta), the scutal microtrichial pattern (postsutural silvery microtrichial area extending anteriorly beyond level of dorsocentral seta and with deep medial notch, but not connected to presutural microtrichose band or spots), and leg color (entirely yellow).

Description. Body 4.0–6.5 mm long, dark brown and yellow. Wing 4.2–5.0 mm long, 1.8–2.3 mm wide. Mesonotum 1.95–2.60 mm long. Setae dark red brown to black.

Head. Yellow, with ocellar tubercle and most of occiput, but not bordering eye, brown. Ventral 2/3 of face and parafacial, most of gena and postgena white. Face dorsomedially, and gena sometimes with reddish brown spot. Frons with 2 frontal setae (3 on 1 side in 2 specimens) and 2 orbital setae (3 on 1 side in 1 specimen). Ocellar, postocellar, and genal setae moderately well developed. Facial ridge with row of 4–6 moderately well-developed setae. First flagellomere ca. 1.5 × as long as wide (on medial side). Arista pubescent.

Thorax. Dorsum entirely dark brown except margin of postpronotal lobe bordering scutum yellow; postpronotal seta on brown area. Scutum shiny, nonmicrotrichose except for 3 densely microtrichose areas: narrow band of silvery white microtrichia on posterior part of presutural scutum, with 3 constrictions or sometimes divided into 3–4 spots; large, somewhat ovoid, postsutural area of microtrichia, mostly silvery white but narrowly brown medially along posterior margin, extending laterally almost to level of intra-alar seta, extending anteriorly beyond dorsocentral seta, with deep medial notch in anterior margin, extending posteriorly to or beyond level of dorsocentral seta; and lateral bimodal ovoid area of blackish microtrichia, extending from transverse suture to posterior corner lateral to supra-alar seta, nearly divided by narrow bare area extending to postalar seta. Scutal setulae pale brown to brown on nonmicrotrichose areas, larger, slightly stouter, and yellow on and bordering silvery white microtrichose areas. Scutellum strongly convex, largely shiny, nonmicrotrichose except for semicircular basomedial area of brown microtrichia, its medial margin extending slightly posterior to level of basal scutellar seta, but not extending to it laterally; with numerous acuminate, brown setulae on nonmicrotrichose area. Pleura white microtrichose except small bare spot ventral to katepisternal seta; mostly yellow to pale brown. Anepisternum usually with narrow white band on dorsal margin and another medially. Katepisternum brown except dorsal margin. Subscutellum and mediotergite brown; subscutellum with brown microtrichia; mediotergite with dense white microtrichia. Setulae on propleuron, anepisternum, anepimeron and dorsal margin of katepisternum moderately long, white or pale yellow. Following setae well developed: postpronotal, 2 notopleural, presutural and postsutural supra-alar, intra-alar, postalar, dorsocentral (aligned slightly posterior to postsutural supra-alar seta), acrostichal, 2 scutellar, anepisternal, katepisternal and anepimeral.

Legs. Entirely yellow.

Wing (Fig. 1B). Base mostly brown, cell c and basal cells with hyaline spots or streaks. With 4 brown bands: First band extending from base of pterostigma to apex of cell a1+cu2; second band broadly connected to first band from pterostigma to vein M, covering crossveins R-M and DM-Cu; third and fourth bands fused basally and broadly connected to second band from costa to vein R_{2+3}, separated distally by hyaline area extending to or almost to vein R_{2+3}; fourth band separated from costa by narrow, irregular hyaline markings. Distal third of pterostigma and often area posterodistal to it in cell r1 paler than base of pterostigma.

*Abdomen***.** Mostly brown. Base of syntergite 1+2 usually yellow. Syntergite 1+2 and tergite 4 with broad apical bands of silvery white microtrichia.

Male terminalia. Similar to *C. loranthi* (see Hardy, 1967, fig. 3). Surstyli short, together with epandrium nearly circular in outline in posterior view, anterior and posterior lobes barely differentiated. Glans without membranous basal lobe; subapical lobe long and rodlike, trumpet shaped apically.

Female terminalia (Fig. 2A). Oviscape 1.7 mm long, mostly pale brown, distal fourth dark brown. Eversible membrane (Fig. 2B) dorsally and ventrally with short taeniae on basal 0.16, remaining part evenly covered by short, triangular denticles, gradually decreasing in size distally. Aculeus (Figs. 2C–D) 1.7 mm long, slender, mostly parallel-sided; tip 0.40 mm long, 0.09 mm wide, nonserrate, elongate triangular, gradually tapered. Two spermathecae (Fig. 2E) tear-drop shaped.

Type specimens. Holotype ♀ (Museum National d'Histoire Naturelle, Paris; USNM00214093), **NEW CALEDONIA**: Rivière Bleue Prov. Pk., km 25.8 Riv. Bleue road, 22°10'34"S 166°30'17"E, 213 m, Malaise trap across forest path, 5–16 Nov 1992, D.W. Webb & E. & M. Schlinger. Paratypes: **NEW CALEDONIA**: Rivière Bleue Prov. Pk., 213 m, Malaise trap across forest path, 20–28 Nov 1992, E. & M. Schlinger & D.W. Webb, 2♂ (INHS USNM00214095–96); Rivière Bleue Prov. Pk., km 21.9 Riv. Bleue road, 290 m, Malaise trap in Maquis, 18–20 Nov 1992, D.W. Webb, 1♂ (QM USNM00214094); Rivière Bleue Prov. Pk., Trail to Upper Riv. Bleue, 290 m, Malaise trap across forest path, 16–19 Nov 1992, D.W. Webb, 1♂ (USNM USNM00214097); same, 5–16 Nov 1992, 1♂ (MNHN USNM00214098); Rivière Bleue Pr. Pk., 30 km NW Yaté, 21 Dec 1991, M.E. Irwin, 1♂ (USNM USNM00214099). Prov. Sud, Mt. Khogis, 17 km NNE Nouméa, 425 m, Malaise trap across path in rainforest, 24–28 Jan 1996, M.E. Irwin, D.W. Webb & E.I. Schlinger, 1♂ (INHS USNM 00214092).

Etymology. This species is named for Ev Schlinger, one of the collectors of the type series.

Dioxyna conflicta (Curran)

Ensina conflicta Curran, 1929: 11.

Specimens Examined. NEW CALEDONIA: Poindimie beach area, 12 Nov 1992, E. & M. Schlinger, 1♂ 1♀ (INHS; USNM00214244-45).

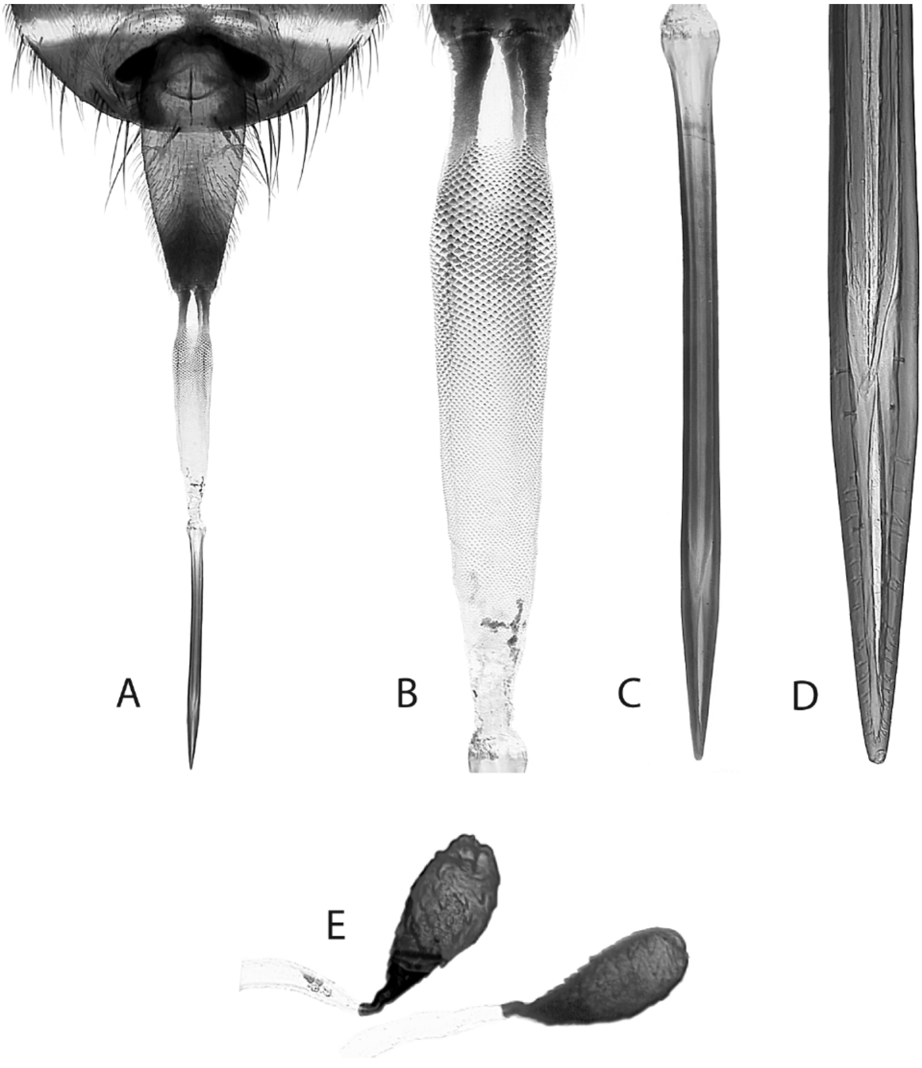

Figure 2. *Ceratitella schlingeri*. **A**. female terminalia; **B**. eversible membrane; **C**. aculeus; **D**. aculeus tip; **E**. spermathecae.

Dioxyna sororcula (Wiedemann)

Trypeta sororcula Wiedemann, 1830: 509.

Comments. This species is widespread in the palaeotropics, but this is the first record for New Caledonia.

Specimens Examined. NEW CALEDONIA: Mt. Do, 14 km NE Bouloupari, 950 m, 31 Oct 1992, D.W. Webb, 1♀ (INHS; USNM00214242). Mt. Khogis, 500 m, 1 Nov 1992, E. & M. Schlinger, 1♂ (INHS; USNM 00214243). Rivière Bleue Prov. Park, 290 m, Malaise trap across forest pass, 3 Nov 1992, M.E. Irwin & D.W. Webb, 2♂ 2♀ (INHS; USNM00214238-41).

Dirioxa pornia (Walker)

Trypeta pornia Walker, 1849: 1039.

Specimens Examined. NEW CALEDONIA: Mt. Pinae Trail, 200 m, MT, 11–25 Nov 1992, E. & M. Schlinger & D.W. Webb, 1♀ (USNM; USNM00214232). Prov. Sud, Camp Brun, 15 km WNW Boulouparí, 100 m, Malaise trap across stream, 16–22 Jan 1996, M.E. Irwin & D.W. Webb, 1♂ (USNM; USNM00214231). Prov. Sud, Mt. Khogis, 17 km NE Nouméa, 22°10'34"S 166°30'17"E, Malaise trap across path in rainforest, 425 m, 24–28 Jan 1996, M.E. Irwin, D.W. Webb & E.I. Schlinger, 3♀ (INHS; USNM00214234–36). Prov. Sud, 9.7 km NW Sarraméa, 21°35'12"S, 165°46'53"E, 500 m, Malaise trap along *Melaluca* path, 22–24 Jan 1996, M.E. Irwin, D.W. Webb & E.I. Schlinger, 1♀ (USNM; USNM00214233).

Euphranta hardyi Norrbom & Hancock, **new species**
(Figs. 1C, 3A–E)

Diagnosis. This species is similar in wing pattern to *E. hainanensis* (Zia), *E. mikado* (Matsumura), *E. oshimensis* (Shiraki), and *E. perkinsi* Hardy, but in those species the band crossing DM-Cu is either separated posteriorly from the band over R-M, or separated anteriorly from the subapical band, or both. *Euphranta hainanensis* also has the face entirely brown and the band crossing the pterostigma and R-M broader anteriorly, *E. mikado* lacks the white area on the anepisternum (USNM specimen examined), and *E. perkinsi* is mostly yellow or rufous (Hardy, 1983). *Euphranta ternaria* Permkam & Hancock is also similar in wing pattern but all of the bands are separated and the pterostigma has a large medial hyaline area. The aculeus of *E. hardyi* resembles those of *E. athertonia* Permkam & Hancock, *E. linocierae* Hardy, and *E. songkhla* Hancock & Drew, but the tip is more elongate and tapered than in *E. athertonia* and the base of the tip is more rounded than in *E. linocierae* and *E. songkhla*. *Euphranta hardyi* further differs from *E. athertonia* by the white area on the anepisternum, and its male fore basitarsus is not flattened as in *E. linocierae* and *E. songkhla*.

Description. Body 7–9 mm long, mostly dark brown to black. Wing 7.1–7.7 mm long, 2.8–3.3 mm wide. Mesonotum 3.4–3.8 mm long. Setae black.

Head. Face yellow, with medial and lateral brown spots or brown band on ventral margin, ventral part of antennal grooves sometimes also brown (face entirely yellow in male, in which color may not be fully developed). Parafacial ventrally, and large area bordering eye on gena brown. Frons brown except orbital plate, vertex, and narrowly anterolaterally. Occiput and postgena yellow, sometimes whitish bordering eye. Frons with 2 large frontal setae and 1 large orbital seta. Ocellar seta absent. Postocellar seta slightly larger than largest postocular setae. First flagellomere 3.2 × as long as wide. Arista long plumose, longest rays as long as width of first flagellomere.

Thorax. Mostly dark brown to black. Anepisternum (Fig. 3A) with posterodorsal corner bright white, not extending posterior to phragma. Postpronotal lobe, propleuron, posterior half of notopleuron, medial postsutural ovoid spot on scutum, extending to or almost to acrostichal seta posteriorly and almost to dorsocentral seta laterally, yellow. Scutum sometimes also with diffuse orange medial vitta. Scutellum with margin of disk and sides yellow, sometimes fading to white apically. Thorax entirely microtrichose except large anteroventral area on anepisternum, small spot on katepisternum ventral to katepisternal seta, and small medial areas on katatergite, meron, and mediotergite. Scutum with broad medial stripe of denser microtrichia extending laterally to level of acrostichal seta, sometimes slightly broader and denser anteriorly. Following setae well developed: lateral scapular, postpronotal, 2 notopleural, postsutural supra-alar, intra-alar, postalar, dorsocentral (aligned 0.57–0.67 distance from postsutural supra-alar seta to intra-alar seta), acrostichal, basal and apical scutellar, 2 anepisternal (more ventral seta much shorter and weaker), katepisternal, and anepimeral; presutural supra-alar seta absent. Anatergite with numerous long fine yellowish hairs.

Legs. Coxae and trochanters yellow; femora brown medially, most extensively on fore femur, hind femur usually with only anteromedial brown spot; tibiae and tarsi brown. Femora ventral setae not spinelike. Male fore basitarsus not swollen or flattened.

Wing (Fig. 1C). Hyaline with 4 dark brown bands. Area bordering crossvein H and posterior to it in cell br, narrow anterior margin of cell c, and anterior margin of cell bcu faint brown to yellow. Basal dark brown band narrow, covering node of Rs, BM-Cu, and Cu_2, extending from vein R_1 to slightly into cell cu1. Second dark brown band broad, covering all of pterostigma and R-M, broadly connected to third band on posterior wing margin. Hyaline area between second and third bands at most 2/3 width of bands (measured along vein R_{4+5}), extended from costa almost to vein Cu_1. Third dark brown band covering DM-Cu, broadly connected to fourth band anteriorly. Hyaline area between third and fourth bands at most 0.4 × as wide as third band (measured along vein M), extended from posterior margin to vein R_{4+5} or vein R_{2+3}. Fourth dark brown band entirely brown (without hyaline markings within it), very broad, apical hyaline spot extended broadly into apical part of cell r4+5 but not extended to apex of vein M.

Abdomen. Mostly brown, with medial yellow vitta from base of syntergite 1+2 to apex of tergite 4. Apex of male tergite 5, and lateral and apical margins of female tergite 6 also yellow.

Male terminalia. Surstyli elongate, 1.5 × height of epandrium.

Female terminalia. Oviscape (Fig. 3B) 1.8 mm long, basal half yellow, distal half brown. Eversible membrane with 2 dorsal and 2 ventral taeniae on basal half, ventral pair much closer together; distal half (Fig. 3C) evenly covered with short, stout, almost conical denticles, gradually shorter posteriorly. Aculeus (Fig. 3D) 0.57 mm long, 0.20 mm wide; tip nonserrate, without teeth or strong steps, nearly parallel-sided on basal fourth, then rapidly tapered (lateral margin concave), distal half slender. Three spermathecae (Fig. 3E) ovoid, tapered basally.

Type Specimens. Holotype ♀ (Museum National d'Histoire Naturelle, Paris; USNM00214890), **NEW CALEDONIA**: Prov. Sud, 9.1 km NW Sarraméa, 21°35'07"S, 165°47'24", 425 m, Malaise trap on forested hillside, 14 Jan 1996, M.E. Irwin, D.W. Webb & E.I. Schlinger. Paratypes: **NEW CALEDONIA**: Mt. Mandjanie, 5.3 km WSW Puébo, 550 m, Malaise trap in tropical forest, 9–26 Nov 1992, D.W. Webb, 1♂ (INHS; USNM00214892). Prov. Sud, 9.1 km NW Sarraméa, 21°35'07"S, 165°47'24"E, 425 m, Malaise trap on forested hillside, 14 Jan 1996, M.E. Irwin, D.W. Webb & E.I. Schlinger, 1♀ (USNM; USNM00214889); 9.1 km NW Sarraméa, 21°35'07"S, 165°48'55"E, 305 m, Malaise trap on forest hillside, 10 Jan 1996, M.E. Irwin, D.W. Webb & E.I. Schlinger, 1♀ (INHS; USNM00214891).

Etymology. This species is named in honor of D. Elmo Hardy, in recognition of his many contributions to the taxonomy of the genus *Euphranta*.

Euphranta leichhardtiae Permkam & Hancock

Euphranta leichhardtiae Permkam & Hancock, 1995: 1151.

Comments. This species was previously known only from Australia (northern Qld. to northeastern NSW). In Australia it breeds in fruit of *Melodorum leichhardtii* (F. Muell.) Benth. (Annonaceae) (Permkam & Hancock, 1995; host as *Rauwenhoffia leichhardtiae*).

Specimens Examined. NEW CALEDONIA: Rivière Bleue Prov. Pk., 213 m, Malaise trap across forest path, 20–28 Nov 1992, E. & M. Schlinger & D.W. Webb, 1♀ (USNM; USNM00214230).

Euphranta lemniscata (Enderlein)

Trypeta lemniscata Enderlein, 1911: 426.

Comments. The 2 males from north of Sarraméa have the discal band narrowly interrupted along vein R_{4+5}, but otherwise resemble specimens of *E. lemniscata* from other areas. This species was recently recorded from New Caledonia by Hancock & Drew (2003).

Specimens Examined. NEW CALEDONIA: Tiea Reserve, 21°07'S 164°57'E, 30 m, at UV light, 4–5 Nov 2001, G. Monteith, 1♂ (QM); Prov. Sud, 1 km N Sarraméa, 21°38'14"S, 165°51'35"E, Malaise trap on forest hillside, 11 Jan 1996 M.E. Irwin, D.W. Webb & E.I. Schlinger, 2♂ (INHS; USNM00214228-29).

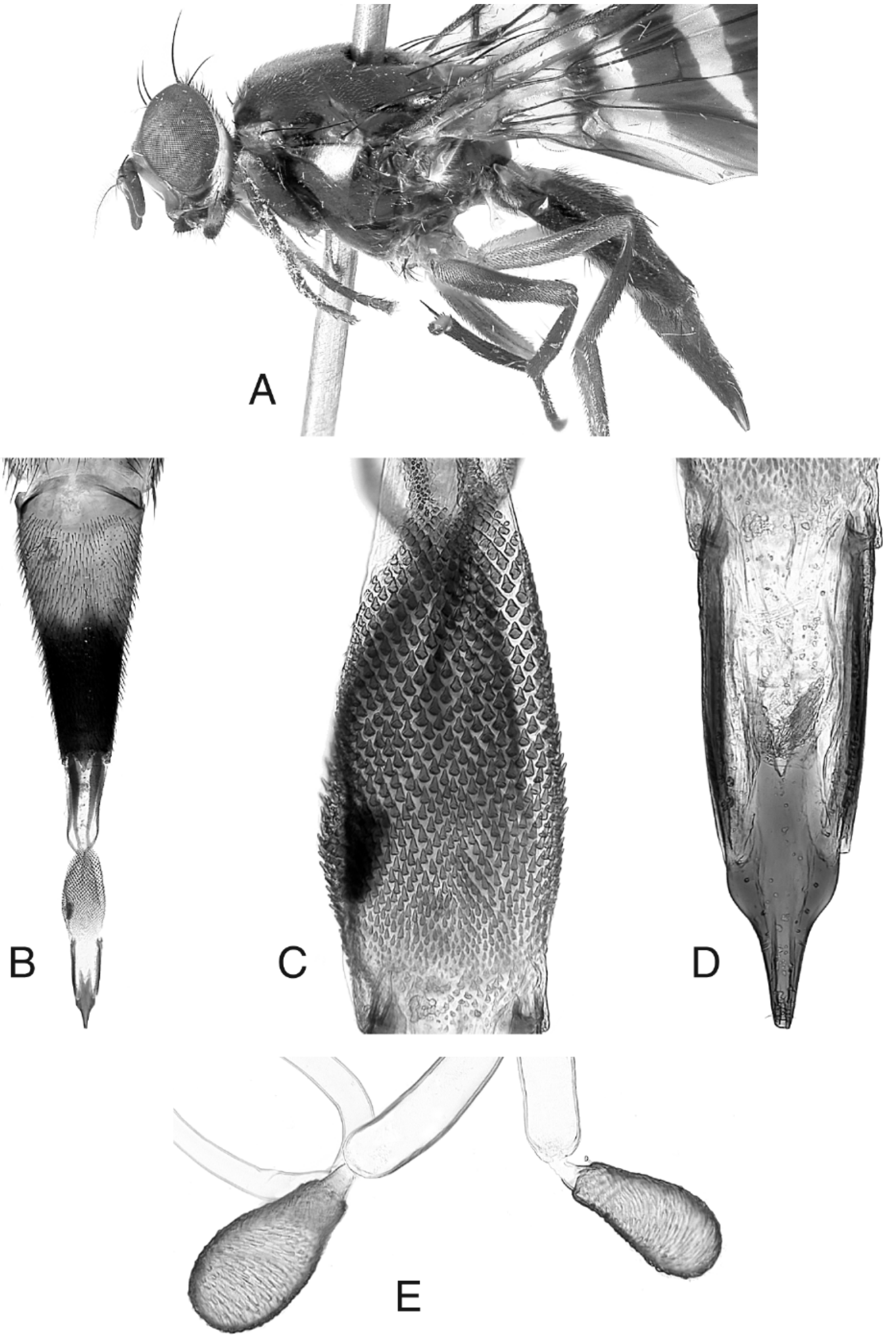

Figure 3. *Euphranta hardyi*. **A**. Lateral habitus; **B**. female terminalia; **C**. distal half of eversible membrane; **D**. aculeus; **E**. spermathecae (2 of 3).

***Soita* sp.**

Comments. The single male, which is lacking mid and hind legs, is the first record of this genus from New Caledonia. It differs from Hardy's (1983) redescription of *Soita psiloides* Walker, currently known only from New Guinea and Australia (Permkam & Hancock, 1995), in having a medial brown mark on the frons and the apices of the radial cells faintly infuscated. Its status needs further study.

Specimens Examined. NEW CALEDONIA: Prov. Sud, 9.3 km NW Sarraméa, 21°35'04"S, 165°47'18"E, 445 m, Malaise trap along forest path, 23 Jan 1996 M.E. Irwin, D.W. Webb & E.I. Schlinger, 1♂ (INHS).

Sphaeniscus atilius (Walker)

Trypeta atilia Walker, 1849: 1021.

Comments. This species is widespread in the palaeotropics but this is the first record for New Caledonia.

Specimens Examined. NEW CALEDONIA: Prov. Sud, 7.5 km NW Sarraméa, 355 m, Malaise trap in opening in forest, 13 Jan 1996, M.E. Irwin, D.W. Webb & E.I. Schlinger, 1♀ (USNM; USNM00214237).

Sphenella ruficeps (Macquart)

Urophora ruficeps Macquart, 1851: 261.

Specimens Examined. NEW CALEDONIA: Mt. Khogis, 17 km NE Nouméa, 500 m, Malaise trap across forest pass, 30 Oct 1992, M.E. Irwin & D.W. Webb, 1♀ (INHS; USNM00052395).

Tetreuaresta obscuriventris (Loew)

Trypeta obscuriventris Loew, 1873: 313.

Comments. This Neotropical species was introduced to Hawai'i and Fiji for biological control of the weed *Elephantopus mollis* (Asteraceae). It also occurs on Tonga (see Specimens Examined) and is here reported for New Caledonia.

Specimens Examined. FIJI: Viti Levu, Korotongo, 0–100 m, Mar 1974, N.L.H. Krauss, 10♂ 15♀ (USNM); Nandarivatu, 850–950 m, 2 Mar 1973, N. L. H. Krauss, 1♀ (USNM); Nandi, 0–100 m, 5 Jun 1973, N.L.H. Krauss, 1♂ (USNM); same, Apr 1974, 8♂ 5♀ (USNM). **NEW CALEDONIA:** Mandjelia Forest, 600–700 m, 9 Nov 1992, E. & M. Schlinger, 1♂ (INHS; USNM00214250). Mt. Khogis, 17 km NNE Nouméa, 500 m, Malaise trap in tropical forest, 15–20 Nov 1992, D.W. Webb, 1♀ (INHS; USNM00052396). Mt. Pinae Trail, 200 m, 11–25 Nov 1992, E. & M. Schlinger & D.W. Webb, 2♂ 7& (INHS) 1♀ (USNM; USNM00214248). Mt. Pinae Trail, below 200 m, MT, 25 Nov 1992, E. & M. Schlinger, 1♂ (USNM; USNM00214247). Prov. Nord, Mt. Mandjélia, 6 km WSW Puébo, 20°24'09"S 164°30'54"E, 545 m, Malaise trap in rain forest, 17 Jan 1996, M.E. Irwin & D.W. Webb, 1♂ (USNM; USNM00214246). Table Unio Road, 21°34'S 165°46'E, 500 m, rainforest, sweeping, 14 Nov 2000, C.J. Burwell, 1♂ 1♀ (QM). Prov. Sud, 7.5 km NW Sarraméa, 355 m, Malaise trap in opening in forest, 11 Jan 1996, M.E. Irwin, D.W. Webb & E.I. Schlinger, 1♀ (USNM; USNM00214249). 9.1 km NW Sarraméa, 21°35'07"S 165°47'24"E, 425 m, Malaise trap on forested hillside, 18–19 Jan 1996, M.E. Irwin, D.W. Webb & E.I. Schlinger, 1♂ (INHS; USNM00214251). **TONGA**: Tongatapu, Faheta, 0–100 m, 27 Nov 1969, N.L.H. Krauss, 2♂ (USNM); Nuku'alofa, 0–50 m, Oct 1969, N.L.H. Krauss, 2♂ 3♀ (USNM); same, 0–20 m, Mar 1971, 10♂ (USNM); same, 0–100 m, Mar 1974, 5♂ 5♀ (USNM).

Acknowledgments

We thank Steve Gaimari and Don Webb (INHS) for arranging the loan of most of the study material. Lucrecia Rodriguez produced the wing images. We thank Ian White, Wayne Mathis, Gary Miller, and F. Christian Thompson for reviewing the manuscript.

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Bibionidae (Diptera) of New Caledonia

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Abstract

Five species of Bibionidae are recognized as occurring in New Caledonia: *Bibio illaudatus* Hardy, *Dilophus arboreus* n. sp., *D. proxilus* n. sp., *Plecia imocellata* n. sp., and *P. lusca* n. sp. A key to the Bibionidae of New Caledonia is provided and the subgenus *Plecia* (*Heteroplecia*) Hardy is discussed.

Introduction

Only 1 species of Bibionidae, *Bibio illaudatus* Hardy (1961: 94), was previously recorded from New Caledonia. Since that report over 40 years ago, additional specimens have accumulated and the current review of the bibionid fauna recognizes 5 species with 4 described as new. New Caledonia is well known for having a high percentage of endemic flora and fauna (Myers, 1988; Najt & Grandcolas, 2002) and thus it is not surprising that all of the bibionid species reported herein are apparently restricted to the islands.

Materials and Methods

Morphology and orientation primarily follows McAlpine (1981). Description of male synsternogonocoxite (ventrally fused gonocoxites + hypandrium) is in ventral view, epandrium in dorsal view, lateral lobe of gonocoxite in lateral view, female tergite 9 in dorsal view, and female sternite 8 in ventral view, unless otherwise specified.

The following persons and collections made material available for study [acronyms follow Samuelson & Evenhuis (2003)]: Neal Evenhuis, Keith Arakaki, and Tino Gonsalves, Bernice P. Bishop Museum, Hawaii (BPBM); Nigel Wyatt, The Natural History Museum, London (BMNH); Don Webb and Mike Irwin, Illinois Natural History Survey Insect Collection, (INHS); Loïc Matile, Eric Guilbert, Muséum National d'Histoire Naturelle, Paris (MNHN); Philip Clausen, University of Minnesota Insect Collection, St. Paul (UMSP); F. Christian Thompson, National Museum of Natural History, Smithsonian Institution (USNM).

Systematics

Key to the Bibionidae of New Caledonia

1\. Rs unbranched (Figs. 6, 12); fore tibia with an apical circlet of spines (Figs. 2, 9, 10) or a strongly developed apical spine and variously developed apical spur (Fig. 1), ocelli present (Figs. 4, 14–16) 2
–. Rs bifurcate; fore tibia simple (with only a minute apical spur), ocelli absent (Fig. 29) .... **Plecia** ... 4

2\. Fore tibia with a strongly developed apical spine and weakly developed apical spur (Fig. 1) .... ***Bibio illaudatus***
–. Fore tibia with an apical circlet of spines (Figs. 2, 9, 10) .... ***Dilophus*** ... 3

3. Hind basitarsus of male slightly swollen (Figs. 7, 8), base of M and m-cu cross vein present, sclerotized rostrum of male 1/2–3/4 the length of lower region of compound eye (Fig. 14, 16), rostrum of female subequal to rest of length of head (Fig. 15), medial spines of fore tibia arranged in a 2:2 or 4 pattern (Figs. 9, 10), wing 3.5–4.0 mm .... ***D. proxilus***

–. Hind basistarsus of male slender elongate (Fig. 3), base of M and m-cu absent (Fig. 6), rostrum short in both sexes (Fig. 4), medial spines of fore tibia arranged in a 2:2:1 or 2:3 pattern (Fig. 2), minute species (wing 2.6 mm) .... ***D. arboreus*, n. sp.**

4. Dorsum of thorax orange or brown-orange 5

–. Entire thorax black .... ***Plecia* sp.**

5. Male with lateral lobe of gonocoxite digitate (Figs. 17, 18) and gonostylus simple (Fig. 20). Female terminalia as in Fig. 22 .... ***Plecia imocellata*, n. sp.**

–. Male with lateral lobe of gonocoxite undeveloped (Fig. 23), gonostylus bifurcate and complex (Figs. 25, 26). Female terminalia as in Fig. 28 .... ***Plecia lusca*, n. sp.**

Bibio illaudatus Hardy

(Fig. 1)

Bibio illaudatus Hardy, 1961: 94. Holotype male (USNM), NEW CALEDONIA: Hienghene, 7 Jun. 1944, W. Crabb.

DIAGNOSIS. Hardy (1961) stated that *B. illaudatus* differs from *B. obediens* by having the fore tibial spur short and not more than 1/4 the length of the tibial spine and all femora black. However, some specimens of *B. illaudatus* examined herein have a slightly longer tibial spur (ca. 1/4–1/3 the length of the tibial spine) which overlaps the variation observed for *B. obediens*; specimens of *B. obediens* examined had spurs 1/3 to nearly 2/3 the length of the spine. The male terminalia of *B. illaudatus* and *B. obediens* are nearly identical; the gonostylus and epandrium, entirely so. Only the narrower cleft of the posterior margin of the synsternogonocoxite and the more convex (in dorsal or ventral views) lateral portion of the gonocoxites will distinguish the male terminalia of *B. illaudatus* from that of *B. obediens*.

MATERIAL EXAMINED. Holotype and 4 paratypes (USNM) and 1 male paratype (BPBM) of *B. illaudatus* as well as the following specimens of *B. obediens* (det. D.E. Hardy) were examined: Neth. Ind. – American New Guinea Exped., Sigi Camp 1500 m, 22 Feb. 1939, L.J. Toxopeus (BPBM)(1 female); New Guinea (Neth.), Wisselmeren: Enarotadi 2000 m, 5 Aug. 1955, J.L. Gressitt (BMBM)(1 female); New Guinea, Wau, 1750m, 23 Aug. 1965, Malaise trap, J. & M. Sedlacek (BPBM)(1 male); New Guinea: Papua, Owen Stanley Range, Goilala: Bome, 1950m, 1–15 Apr. 1958, W.W. Brandt (BPBM)(1 male).

DISCUSSION. Hardy (1961) discussed the possibility that *B. illaudatus* may be only a subspecies of *B. obediens* Osten Sacken, which was described from New Guinea. Small sample size prevents an adequate study of the inter- and intraspecific variation of *B. illaudatus* and *B. obediens*. Therefore, based upon the material examined herein these taxa are treated as distinct until additional data suggests otherwise. Hardy (1968a) stated that specimens of *B. obediens* were examined from New Hebrides; these specimens have not been examined, but may provide additional insight into the status of *B. illaudatus* and *B. obediens*. Based on Hardy's (1968a) discussion of *B. obediens* it appears that the species concepts of *Bibio* in the entire region (e.g., India, Philippines, New Caledonia, New Guinea) are in question and the genus probably requires a synthetic revision that reexamines all the species that have been described from these areas.

Dilophus arboreus Fitzgerald, **new species**
(Figs. 2–6)

DIAGNOSIS. *Dilophus arboreus* is most similar to *D. tuthilli* from New Zealand, but differs from this species because the head is not strongly modified with the eyes projecting at the front of the head and the face greatly receded (compare Fig. 4 to Hardy, 1953, Fig. 7a). However, it is possible that the unique structure of the head of *D. tuthilli* noted by Hardy (1953) is an artifact of preservation. The 5 paratypes of *D. tuthilli* that were examined (USNM) are pinned and the anterior and ventral surfaces of the head appear to have collapsed when the specimens dried up. Since the specimens of *D. arboreus* are preserved in alcohol (except for the holotype and paratype, which were pointed after treating with hexamethyldisilazane (HMDS) to reduce the collapse of structures (Nation, 1983)), the head is not collapsed and it remains unclear whether the difference in head shape in these taxa is an artifact or not. If the shape of the head is an artifact, these two taxa differ only in minor differences in the shape of the terminalia. In *D. arboreus* the apex of the gonostylus is slightly more blunt (more acute in *D. tuthilli*) and the dorsal sclerite of the paramere of *D. arboreus* is slightly broader than in *D. tuthilli* (Fig. 5).

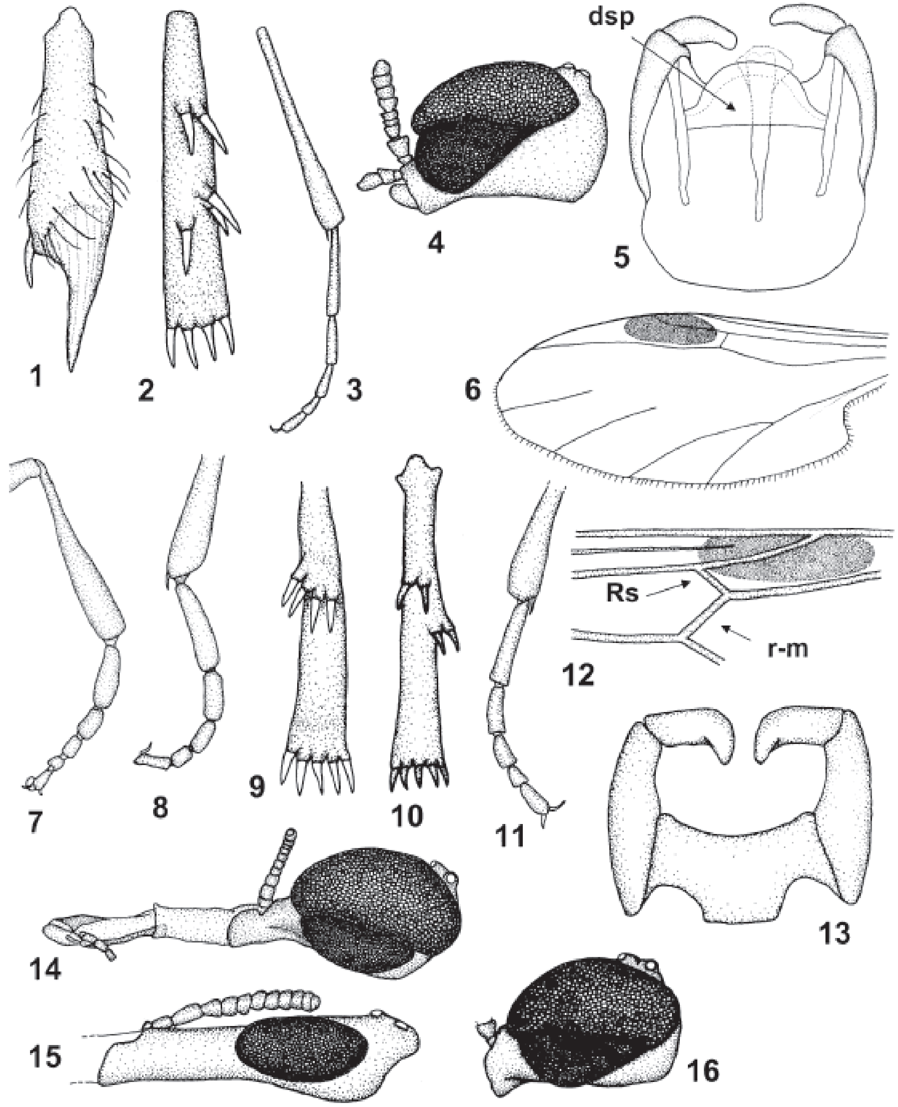
MALE. Head black with short dark setae. Ocelli present. Ocellar tubercle only slightly developed; in lateral view ocelli just above level of compound eye. Sclerotized portion of head anterior to compound eye undeveloped beyond antennae (Fig. 4). Antennae brown with 7–8 flagellomeres; apical flagellomeres 4–5 closely compacted together forming a weak club. When 8 flagellomeres present the apical segment is minute and button-like. Compound eye with minute, dark, erect, sparse hair; lower 1/3 of eye divided into region of smaller facets by a distinct thin sclerotized longitudinal band. Thorax dark brown; dorsum shining with dorsocentral rows and lateral rows of dark setae. Prothoracic comb with 8 spines; medially undivided. Metathoracic comb with 7 smaller spines. Fore coxa yellowish brown, mid and hind coxae brown. All femora clavate, basally yellowish brown and distally brown. Fore tibia brownish yellow with an apical circlet of 7 spines. Fore tibia dorsally with medial spines above the apical set; beginning basally and moving distally there is a pair of dorsal spines, a pair of posterodorsal spines, and then a single dorsal spine (Fig. 2). Occasionally the distal 3 spines appear to be in a single row rather than the most distal spine set off by a small gap. Inner surface of hind tibia with 21–22 (N = 2) sensilla. Mid and hind tibia yellow-brown basally and brown distally. Tarsi brown. Hind basitarsus slender elongate, 9 × as long as wide. Hind tibia subparallel. All legs with short dark setae. Halter light brown. Wing 2.6 mm slightly light brown fumose, veins brown. Pterostigma brown. Radius with short black evenly spaced setae and minute transverse striations. Costa extending almost to wing tip, considerably beyond end of Rs (Fig. 6). Subcosta complete. Base and fork of M absent; only apices of M_1 and M_2 present (Fig 6). M-cu crossvein absent. Wing with evenly spaced microtrichia. Anal lobe well developed. Hind margin of wing with a fringe of setae. Abdomen dark brown with sparse black setae. Posterior margin of epandrium nearly straight; not emarginated. Gonostylus short, thick, slightly tapered apically, apex blunt (Fig. 5).

FEMALE. As in male except the following: Head and thorax brown. Eye dichoptic, undivided. Prothoracic comb with 6–8 spines, metathoracic comb with 8–9 spines. Abdomen weakly sclerotized and abdominal pleurae extensive; sternites often anteromedially excised or entirely longitudinally divided. Ocellar tubercle absent. Inner surface of hind tibia with 24–26 sensilla (N = 2). In dorsal view a thin longitudinal carina present from lateral edge of prothoracic comb to lateral edge of metathoracic comb delineating 2 anterolateral regions of the mesonotum that are yellowish brown and contrast the darker remainder of the dorsum. Hind basitarsus slender elongate, approximately 12 × as long as wide. Wing 2.6 mm.

TYPE SPECIMENS. Holotype male: NEW CALEDONIA: Rivière Bleue (P6), Forêt dense, fogging 21 Oct. 92, Chazeau, Guilbert, Bonnet de Larbogne (MNHN). Paratypes: Same as holotype, 1 female (MNHN).

ADDITIONAL MATERIAL EXAMINED. Same as holotype label, 1 male, 16 females (in alcohol)(MNHN); same as holotype label except 16 Jul. 92, 1 male, 1 female (MNHN).

DISCUSSION. Although all specimens of *D. arboreus* were collected as part of a canopy fogging study in Rivière Bleue Provincial Park (Guilbert, 1997), it seems unlikely that this minute



Figs. 1-16. Bibioninae. **1**, *Bibio illaudatus*, male fore tibia; **2-6**, *Dilophus arboreus*, male; **2**, fore tibia; **3**, hind tibia and tarsi; **4**, head, lateral; **5**, terminalia, dorsal (epandrium removed); **6**, wing; **7-16**, *Dilophus proxilus*; **7-8**, male hind tibia and tarsi; **9-10**, male fore tibia; **11**, female hind tibia and tarsi; **12**, male, portion of wing; **13**, male terminalia, dorsal; **14**, male head, lateral; **15**, female head, lateral; **16**, male head, lateral (excluding mouthparts and antennal flagellum); **dsp** – dorsal sclerite of paramere; **r-m** – radial-medial crossvein; **Rs** – base of radial sector.

species is strictly associated with the canopy. The site (Rivière Bleue P6) at which the type series was collected is characterized as dense evergreen forest on ultramafic alluvium (Guilbert, 1997). The site has been described by Bonnet de Larbogne *et al*. (1991) and the vegetation further characterized by Jaffré & Veillon (1990) and Jaffré *et al*. (1993).

Dilophus arboreus belongs to an apparent complex of species in the south Pacific that are characterized in part by the absence of the base of M and the m-cu crossvein (Hardy 1968a, 1982). Also included in this "group" is *Dilophus tuthilli* (Hardy) (New Zealand), the *D. exiguus* complex (Hardy, 1968a, 1968b) (New Guinea and the Bismarck Islands), and *D. collessi* Hardy, *D. discretus* Hardy, *D. modicus* Hardy, *D. parvus* Hardy, *D. pictipes* Skuse, and *D. sexspinosus* Hardy (Australia).

ETYMOLOGY. The specific epithet is derived from the Latin "*arboreus*" (of trees) as the only specimens of this species were collected via canopy fogging studies.

Dilophus proxilus Fitzgerald, **new species**

(Figs. 7–16)

DIAGNOSIS. *Dilophus proxilus* is most similar to *D. dichromatus* Hardy from New Guinea. Although the male gonostylus of these 2 species is nearly identical, males of *D. proxilus* can be distinguished by having the posterior margin of the epandrium straight rather than with a V-shaped cleft, having 10 rather than 11 antennal flagellomeres, and its slightly smaller size (wing 3.5 mm rather than 4.5 mm). Females of *D. proxilus* can be distinguished by having 10 rather than 11 antennal flagellomeres, thorax with dark stripes rather than entirely orange, legs yellow rather than black, and its smaller size (wing 4.0 mm rather than 6.5–7.0 mm).

MALE. Head black with long black hair. Ocelli present, ocellar tubercle only slightly developed with ocelli projecting just above level of compound eye. Sclerotized portion of head anterior to compound eye 1/2–3/4 length of lower division of compound eye (Figs. 14, 16). Antenna dark brown with 10 flagellomeres; apical flagellomere minute, button-like; basal flagellomere subequal in length to following flagellomere. Compound eye with minute, sparse, erect hair; lower 1/4 eye divided into region of smaller facets. Dorsum of thorax black to dark brown, shining, bare, except long yellow hair forming a dorsocentral pair and a lateral pair of stripes. Prothoracic comb on a well developed ridge, slightly divided medially, with 12 strong spines. Mesothoracic comb on well developed ridge with small spines. Thoracic pleura dark brown to black, bare, shining. Coxae dark brown to black; fore coxa with long yellow to brown hair. Legs dark brown to black; femora always slightly darker, with dense long, dark hair. Fore tibia with an apical circlet of 8 dark brown spines and a longer black anteroventral spur. Fore tibia dorsosubmedially with a row of well developed spines. Submedian spines variable; either 3–4 spines in a single angulate row (Fig. 9) or 2 dorsal and 2 slightly more distal dorsoposterior spines (Fig. 10). Hind tibia apically swollen, about 3 × width base of tibia. Hind basitarsus slightly to moderately swollen, 3–5 × as long as wide (Figs. 7, 8). Halter light brown. Wing 3.5 mm, nearly hyaline, light brown fumose anteriorly. Anterior veins and pterostigma dark brown, posterior veins pigmented, light brown, crossvein m-cu and base of M_{1+2} present. R_1 and R_{4+5} with short, sparse, erect, black, evenly spaced setae; space between hairs much wider than length of seta. Base of Rs 1/4–1/2 length of crossvein r-m (Fig. 12). Abdomen dark brown with long yellow hair laterally and ventrally; tergites 1–3 medially pubescent. Posterior margin of the synsternogonocoxite with broadly rounded median projection. In ventral view, gonostylus robust basally, tapered and narrowly rounded apically; in posterolateral view, narrow, kidney-shaped, apically rounded; in dorsal view simple, elbowed at about half way point with apex pointing anteriorly, apex rounded to slightly truncate (Fig. 13). Epandrium 2 × as wide as long; posterior margin uncleft, nearly straight; anterior margin nearly straight to sinuate (Fig. 13).

FEMALE. Head black with black hair, ocelli present. Ocellar tubercle very weakly developed, ocelli nearly at level of vertex. Compound eye dichoptic, undivided, with minute, erect, sparse hair. Sclerotized portion of head anterior to compound eye elongate, longer than eye, nearly equal to length of remainder of head (Fig. 15). Antenna dark brown, except pedicel light brown, with 10 flagellomeres; basal flagellomere 2 × as long as following flagellomere; apical flagellomere minute, button-like. Humeral ridge dark brown, pronotal lobe brown-yellow. Prothoracic comb on well developed yellow ridge; medially divided to undivided, with 13–14 robust dark brown spines. Mesothoracic comb black to dark brown medially, yellow laterally, with 15 dark brown spines; spines more weakly developed than those of prothoracic comb. Thorax yellow in ground color; dorsum with 3 broad black to dark brown stripes; pleura marked with brown; ventral 2/3 of katepisternum brown. Scutellum brown-yellow. Dorsum of thorax with yellow hair in dorsocentral rows and laterally. Thoracic pleura bare. Fore and mid coxa yellow, hind coxa brown. Trochanter brown. Femora, tibia, and tarsi primarily yellow, except tipped with brown distally; with brown hair. Hind basitarsus slender, elongate, 5 × as long as wide (Fig. 11). Spines of fore tibia likely variable as in male, however, all specimens examined with only a single angulate row of 4 submedian spines. Abdomen brown with yellow hair. Wing 4.0 mm; venation as in male.

TYPE SPECIMENS. Holotype male: NEW CALEDONIA: Rivière des Pirogues, 7–9 Feb. 1984, Pogue & Epstein, black light (UMSP). Paratypes: Same as holotype, 2 males, 1 female (UMSP); New Caledonia, Rivière Bleue Prov. Pk., Trail to Vallée de Pourina, 19 Nov. 1992, 750 m, D.W. Webb, Malaise trap across forest path, 1 male, 1 female (INHS); Nouvelle Calédonie, Mont do, 900–950m, Forêt, 27 Nov. 1983, L. Matile et J. Chazeau, 2 males, 1 female (MNHN).

ADDITIONAL MATERIAL EXAMINED. NEW CALEDONIA: Rivière Bleue (P6), Forêt dense, fogging 21 Oct. 92, Chazeau, Guilbert, Bonnet de Larbogne, 1 male (in alcohol)(MNHN); Mt. Painter, 1360 m., 10 Oct. 1967, J. & M. Sedlacek, 5 males (BPBM); Mt. Koghi, 450–600 m., 4–6 Oct. 1967, J. & M. Sedlacek, 1 male (BPBM); 9.2 km NE Col d'Amieu on Rte. 5, slopes of Mt. Rembai, 375–675 m, 23 Sep.1979, 1 female (BPBM).

ETYMOLOGY. The specific epithet is derived from the Latin "proxilus" (stretched out long) for the elongate rostrum of this species.

***Plecia* (*Heteroplecia*) Hardy**

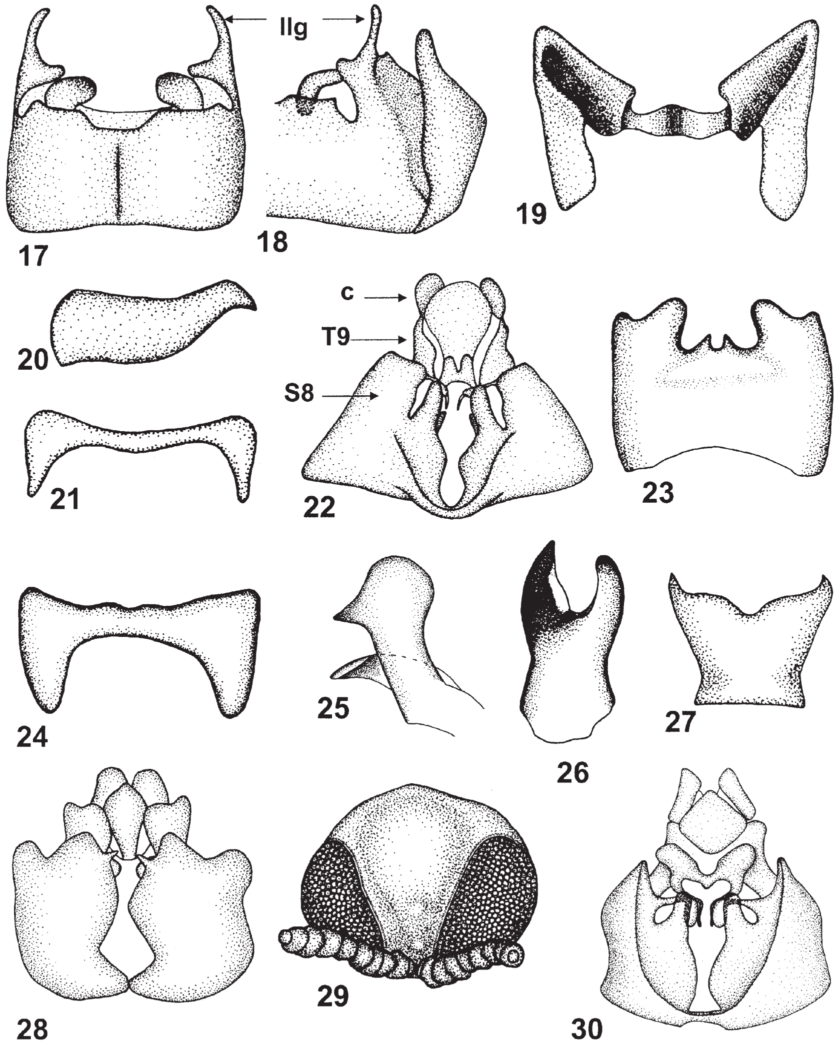
Hardy (1950) erected the monotypic subgenus *Heteroplecia* for the species *Plecia visenda* Hardy from New Guinea. This subgenus is distinguished from the nominate subgenus by the lack of ocelli and an ocellar tubercle. Later, Hardy (1968a) stated that the lack of the ocelli and tubercle is probably only of specific importance and questioned whether *Heteroplecia* should be retained as a distinct subgenus. The 3 *Plecia* species discussed herein are the only other species known to lack these structures and thus would be assigned to *Heteroplecia*. Hardy (1968a) noted that *P. visenda* shows "considerable relationship" to the *decora* complex because of the strongly developed epandrium and short broad ninth sternum, but differ from this complex in a number of aspects. *Plecia lusca* and *P. imocellata* do not fit Hardy's definition of the *decora* complex and are not easily assigned to any of the species groups defined by Hardy (1968a) and Hardy & Delfinado (1969). Considering this, the species described below are tentatively placed in the subgenus *Heteroplecia* until a phylogenetic study of *Plecia* can help to define the subgenera and species groups.

***Plecia imocellata* Fitzgerald, new species**

(Figs. 17–22)

DIAGNOSIS. *Plecia imocellata* is most similar to *P. visenda* and *P. lusca*. Males are easily distinguished by the digitate lateral lobe of the gonocoxite (Figs. 17, 18) and the simple (rather than bifurcate) gonostylus (Fig. 20). Females are distinguished by the shape of sternite 8 (Fig. 22) and tergite 9 (Fig. 21).

MALE. Head brown. Ocelli and ocellar tubercle absent, compound eyes meeting posterodorsally. Compound eye with minute, erect, sparse hair; lower 1/3 of eye divided into region of smaller facets. Face not produced. Clypeus + proboscis brown, short, subequal to length of antenna. Except for orange pedicel, antenna orange-brown to dark brown with 8 flagellomeres; basal flagellomere 2 × length following flagellomere; apical flagellomere minute, nipple-like. Entire thorax



Figs. 17–30. *Plecia*. **17–22**, *P. imocellata*; **17**, male terminalia, ventral; **18**, male terminalia, lateral; **19**, epandrium, dorsal; **20**, gonostylus, lateral; **21**, female tergite 9, dorsal; **22**, female terminalia, ventral; **23–29**, *P. lusca*; **23**, male terminalia, ventral; **24**, male epandrium, dorsal; **25**, male gonostylus, lateral; **26**, male gonostylus, posterior; **27**, female tergite 9, dorsal; **28**, female terminalia, ventral; **29**, female head, dorsal; **30**, *Plecia* sp., female terminalia, ventral; **c** – cerci; **llg** – lateral lobe of gonocoxite; **S8** – sternite 8; **T9** – tergite 9.

opaque orange; dorsum with lateral portion of mesonotum and dorsal 1/2 katepisternum with sparse, short, appressed, pale hair. Scutellum with median light brown stripe. Halter brown apically, orange basally. Wing 6.5–7.0 mm, hyaline; veins and pterostigma light brown. R_{2+3} nearly straight, approximately 1/4 length R_{4+5}. Coxa, trochanter, legs light brown to orange-brown, except apical tarsomeres dark brown; with dense, long, light brown hair. Hind tibia slender. Hind basitarsus slender, elongate, 10 × as long as wide. Abdomen dark brown with dense, long, light brown hair. Posterior and anterior margin of epandrium emarginate leaving only a narrow transverse strip of the epandrium medially (Fig. 19). Gonostylus stout, elongate apically tapered (Fig. 20). Lateral lobe of gonocoxite well developed, digitate (Figs. 17–18). Posterior margin of synsternogonocoxite without median or submedian lobes (Fig. 17).

FEMALE. As in male except: Eye dichoptic, undivided. Frons bulbous, keel-like just posterior of antenna base with a small rounded tubercle. Antenna with 8 flagellomeres. Wing 7.0–8.0 mm. Hind basitarsus 7 × as long as wide. Ventrally, female terminalia as Fig. 22. Tergite 9 as in Fig. 21.

TYPE SPECIMENS. Holotype male: NEW CALEDONIA: Rivière Bleue Prov. Pk., km 21.9 Riv. Bleue road, 3–5 Nov. 1992, 290 m, Malaise trap in Maquis, D.W. Webb, (INHS). Paratypes. NEW CALEDONIA: Same as holotype 6 males (INHS); Mt. Koghi, 500 m, 23–27 Aug. 1967, M. Sedlacek, 1 male (BPBM), same except 23–27 Oct., 500–800 m, J. & M. Sedlacek, light trap, 2 male, 1 female (BPBM); Port Boisé, 13 Aug. 1971, J. Holloway, Acc. #1981.232, 1 male (BPBM); Mt. Stream up Boulari R., light trap, 3 Nov. 1958, C.R. Joyce, 3 males (BPBM); Plaine des Lacs area, 5 Nov. 1958, C.R. Joyce, 1 male, 2 females (BPBM); On Hgts. between Thio & Nakety, 12 Nov. 1958, C.R. Joyce, 3 males, 1 female (BPBM); Mt. Khogis, 500 m, 17 km NNE Nouméa, 5–15 Nov. 1992, Malaise trap in tropical forest, D.W. Webb, 1 male (INHS), same except 30–31 Oct., M.E. Irwin, D.W. Webb, 3 males (INHS), same except 1–3 Nov., M.E. Irwin, D.W. Webb, 1 male (INHS); Rivière Bleue, 30 km NW Yale, Malaise, 29 Sep.–13 Oct. 1986, L.B. deLarbogne, J. Chazeau, A. & S. Tiller, Station Parc 5, collection # 216, 3 males (INHS).

ADDITIONAL MATERIAL EXAMINED. NEW CALEDONIA: Pic du Pin, 300 m, Site 69, 06880/75385, J.D. Holloway, 8 Aug. 1971, swept *Nothofagus* forest, B.M. 1971-507, 1 female (BMNH).

ETYMOLOGY. The specific epithet is derived from the Latin "*im-*" (without) + "*ocellatus*" (having little eyes) describing the lack of the ocelli.

Plecia lusca Fitzgerald, **new species**

(Figs. 23–29)

DIAGNOSIS. Males of *P. lusca* are most similar to *P. visenda* and *P. imocellata*, but can be distinguished by the bifurcate gonostylus (Figs. 25–26), lack of a lateral lobe of the gonocoxite (Fig. 23), and posterior margin of the synsternogonocoxite developed into a pair of small median lobes (Fig. 23). Females can be distinguished by the shape of sternite 8 (Fig. 28) and tergite 9 (Fig. 27).

MALE. Head dark brown. Eyes holoptic, meeting along entire margin of vertex; ocelli and ocellar tubercle absent. Compound eye with sparse, minute, pale hair; not divided into 2 regions of different-sized facets. Antenna brown-orange with 8 flagellomeres; apical flagellomere minute and nipple-like. Palps orange-brown, with 4 segments. Clypeus + proboscis dark brown, short, 1/2 length of antenna. Thorax opaque orange-brown; anepisternum and portions of surrounding thoracic pleurae tinged with dark brown. Femur orange-brown basally, becoming slightly darker distally. Tibia and tarsi orange-brown to brown; distal tarsomeres dark brown. Hind basitarsus slender, elongate, 7 x as long as wide. Abdomen brown with orange tinge, darker posteriorly. Wing 4.0–5.0 mm, hyaline to light brown fumose, stigma and veins brown. R_{2+3} 1/3 length R_{4+5}, nearly straight, at 45 degrees to R_{4+5}. Halter orange-brown basally, light brown apically. Posterior margin of epandrium nearly straight, except 2 slight humps medially (Fig. 24). Anterior margin of epandrium strongly excavated; cleft nearly 3/4 length of epandrium (Fig. 24). Inner surface of epandrium lacking clumps of setae. Posterior margin of synsternogonocoxite developed into 2 pairs of sublateral lobes (submedian lobes of Hardy & Delfinado 1969) and a pair of small, slender, digitate median lobes (Fig. 23); the inner pair of sublateral lobes slightly larger. Synsternogonocoxite with a posterior median triangular membranous area which is widest anteriorly and terminates at the median lobes of the posterior margin of the synsternogonocoxite (Fig. 23). Lateral lobe of gonocoxite undeveloped. Epandrium and synsternogonocoxite very narrowly fused anterolaterally. Gonostylus bifurcate; in posterior view inner lobe rounded, outer lobe acute (Fig. 26); in lateral view inner lobe evenly curved downward, apically acute, outer lobe chicken-head shaped (Fig. 25).

FEMALE. As in male except as follows: Eye dichoptic, undivided. Vertex and frons bulbous with 2 small, rounded, tubercles anteromedially (Fig. 29). Wing 5.0–6.0 mm. Sternite 8 divided medially; the inner margin sinuous with an inward and posteriorly directed, small, tooth-like lobe posteriorly (Fig. 28). Posterior margin of sternite 8 with a broadly rounded lateral lobe, and a broad apically rounded median lobe (Fig. 28). In dorsal view tergite 9 whale-tail shaped; basally constricted, apically expanded; posterior margin with broad, shallow, V-shaped excavation; lateral lobes apically acute (Fig. 27).

TYPE SPECIMENS. Holotype male: NEW CALEDONIA: Plaine des Lacs 5 km. E. Grand Lac, Jan. 22–25 1984, Pogue & Epstein, black light, (UMSP). Paratypes. Same data as holotype, 11 males, 11 females (7 pairs in copula) (UMSP).

ADDITIONAL MATERIAL EXAMINED. In addition to the type material listed above, the following specimens were examined: Nouvelle Calédonie, Rivière Bleue, 20 Feb. 1990, Michel Boulard réc., 2 males, 2 females, (2 pairs in copula) (MNHN).

ETYMOLOGY. The specific epithet is derived from the Latin “lusc” (half blind) describing the lack of ocelli.

Plecia sp.
(Fig. 30)

MATERIAL EXAMINED. NEW CALEDONIA: On Hgts. between Thio & Nakety, 12 Nov. 1958, 1 male (BPBM); Rivière Bleue Prov. Pk., 30 km NW Yaté, 270 m, 27 Dec. 1991, M.E. Irwin, D.W. Webb, Malaise trap across forest path, 1 female (INHS).

DISCUSSION. Among the material examined there was one female and one male which had the entire thorax black. The female terminalia (Fig. 30) was similar to, but slightly different from *P. imocellata* and this specimen may represent an undescribed species. The male with the black thorax is not associated with this female, was collected from a different locality, and is missing the tip of the abdomen. It was collected from the same locality and date as a series of *P. imocellata*. Considering this, it is possible that the male specimen represents a black morph of *P. imocellata*. However, additional material is needed to resolve the identity of both of these specimens.

Other Bibionidae that may occur in New Caledonia

The known limits of geographic distribution of *Plecia amplipennis* Skuse is the Bismarck Archipelago and New Guinea in the north and New South Wales, Australia in the south. The relatively widespread range of this species and occurrence on adjacent Vanuatu make it possible that it may also occur in New Caledonia. This species is distinguished from the New Caledonian *Plecia* species by the presence of ocelli and differences in the male terminalia (Hardy, 1968a; Fig. 15).

Acknowledgments

I sincerely thank Boris C. Kondratieff, Colorado State University, and Darlene D. Judd, Oregon State University for the use of facilities and equipment. Thanks also to Eric Guilbert, Muséum National d’Histoire Naturelle, for providing information on the canopy fogging studies, Dan Bickel, Australian Museum, for his help with locating New Caledonian material, and persons listed with collections who made material available for study. My visit to the National Museum of Natural History, Smithsonian Institution, was supported by the Samuel Wendell Williston Diptera Research fund.

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A Revision of the Shore-fly Genus *Trimerogastra* Hendel (Diptera: Ephydridae)

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Abstract

The species of *Trimerogastra* Hendel, which occur along maritime coasts of the Oriental and Australasian Regions, are revised. Included are 5 species of which two are newly described and one is recognized but not named for lack of a male. The new species are (type locality in parenthesis): *T. hardyi* (Australia. Queensland: Cairns) and *T. mcalpinei* (Australia. New South Wales: Cornulla (34º2.1'S, 151º9.1'E)). Illustrations and descriptions are provided for structures of the male terminalia for all species for which males are available. One new synonym, *Pseudopelina setosa* Miyagi (= *Tetramerogastra fumipennis* Hendel), is also documented. In addition to description of the genus and species, the tribe Gymnomyzini is diagnosed and a key to genera is included.

Introduction

Many shore-fly genera are notable for their ability to tolerate and proliferate in inimical environments such as pools of crude petroleum, hypersaline lakes, or the hot effluent of geysers (Foote, 1995; Oldroyd, 1964). Other ephydrid genera include numerous species that are often abundant or are geographically widespread and are thus also relatively well known. A few genera, however, largely remain unstudied, being represented by one or just a few species and frequently by few specimens. The latter conditions characterize the genus *Trimerogastra* Hendel, which is being revised for the first time in this paper. We dedicate this revision to the memory and friendship of D. Elmo Hardy, our colleague and mentor, and who encouraged our research in dipteran systematics.

Hendel (1914) described *Trimerogastra* in the beginning of the 20th century. Aside from Hendel's original description and Cresson's faunal review (1945), which included the synonymy of *Tetramerogastra* Hendel with *Trimerogastra,* the genus received scant attention or even mention, except for its inclusion in recent catalogs (Cogan & Wirth, 1977; Cogan, 1984; Mathis, 1989; Mathis & Zatwarnicki, 1995). Miyagi (1977) described *Pseudopelina,* later found to be congeneric with *Trimerogastra* (Zatwarnicki, 1991), in his faunal review of the Ephydridae of Japan. Nothing has been published about the immature stages or natural histories of the species included in *Trimerogastra,* and what we know about the morphology of the genus is limited primarily to external features. With the availability of additional specimens, sometimes representing new species from more widespread localities, we are revising this genus to complement our ongoing research on genera of the tribe Gymnomyzini (Mathis *et al*., 1993, *Mosillus* Latreille; Mathis, 1986, *Placopsidella* Kertész; Mathis & Zatwarnicki, 1990a, *Chlorichaeta* Becker; Mathis & Zatwarnicki, 1993, *Athyroglossa* Loew from the western Palearctic).

As part of our revisionary treatment, we are also including structures of the male terminalia, which have not been generally well studied. Miyagi (1977) provided the only genitalic illustrations available, and these are limited to external structures (posterior view of epandrium, cerci, and surstyli) of the single species treated in his faunal review of Japanese shore flies.

Prior to this revision, 4 names were available in *Trimerogastra* (Mathis & Zatwarnicki, 1995). These species-group names in chronological order are: (1) *T. cincta* Hendel (1914), the type species of *Trimerogastra,* (2) *T. fumipennis* (Hendel, 1914), the type species of *Tetramerogastra,* (3) *Trimerogastra longivena* Bezzi (1928), which was subsequently transferred to *Allotrichoma* (Mathis, 1989), and (4) *T. setosa* (Miyagi, 1977), the type species of *Pseudopelina* Miyagi and herein reported to be the junior synonym of *Tetramerogastra fumipennis.* We also add herein 2 new species and a third species, which will remain unnamed, making a total of 5 species currently in the genus.

Methods and Materials

The descriptive terminology, with the exceptions noted in Mathis (1986) and Mathis & Zatwarnicki (1990a), follows that published in the Manual of Nearctic Diptera (McAlpine, 1981). Because specimens are small, usually less than 3.5 mm in length, study and illustration of the male terminalia required use of a compound microscope. Although here we follow the terminology for most structures of the male terminalia that other workers in Ephydridae have used (see references in Mathis, 1986; Mathis & Zatwarnicki, 1990a, 1990b), Zatwarnicki (1996) now uses alternative terms (gonostylus, medandrium) that are based on the “hinge” hypothesis for the origin of the eremoneuran hypopygium. The terminology for structures of the male terminalia is provided directly on Figs. 1–2, 5–10 and is not repeated for comparable illustrations of other species. The species descriptions are composite and not based solely on the holotypes. One head and two venational ratios that are used in the descriptions are defined below (all ratios are based on three specimens (the largest, smallest, and one other). Gena-to-eye ratio is the genal height measured at the maximum eye height divided by the eye height. Costal vein ratio: the straight line distance between the apices of R_{2+3} and R_{4+5}/distance between the apices of R_1 and R_{2+3}. M vein ratio: the straight line distance along vein M between crossveins (dm-cu and r-m)/distance apicad of dm-cu.

Although many specimens for this study are in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), we also studied numerous specimens that are deposited in the following collections:

AMS	Australian Museum, Sydney, Australia.
ANSP	Academy of Natural Sciences of Philadelphia, Pennsylvania, USA.
BMNH	The Natural History Museum, London, England.
DEI	Deutsches Entomologisches Institut, Eberswalde, Germany.
HNHM	Hungarian Natural History Museum, Budapest, Hungary.
HUS	Hokkaido University, Sapporo, Hokkaido, Japan.
KBIN	Royal Belgian Institute of Natural Sciences, Brussels, Belgium.
NMW	Naturhistorisches Museum, Vienna, Austria.

Systematics

Tribe Gymnomyzini Latreille

Gymnomyzini Latreille, 1829: 536 (as Gymnomyzides). Type genus: *Gymnomyza* Fallén, 1810 (= *Mosillus* Latreille, 1804).

Gymnopini Cresson, 1922: 326. Type genus: *Gymnopa* Fallén, 1820 (= *Mosillus* Latreille, 1804). Mathis, 1986: 4–5 [diagnosis].

Diagnosis. The tribe Gymnomyzini is distinguished from other tribes of the subfamily Gymnomyzinae by the following combination of characters: Body extensively shiny black, although with some gray to whitish microtomentum on dorsum; posterior margin of gena sharply angulate; gena with fine pale setulae. Scutellum with 2 pairs of marginal setae. Foreleg normally developed, slender. Abdominal tergites 2–4 subequal in width, microtomentose, but more or less smooth.

Description. Small to moderately large shore flies, body length 1.20–4.30 mm; body extensively shiny black, although with some gray to whitish microtomentum on dorsum.

Head: Fronto-orbital setae reclinate and proclinate or absent; reclinate fronto-orbital seta usually inserted slightly anterior to larger, proclinate fronto-orbital seta. Arista either bare to macropubescent, if pectinate, rays shorter than 1/2 height of flagellomere or arista pectinate dorsally. Median facial area and lower facial margin without setae; facial setae inserted in more or less vertical series, parallel with parafacial. Posterior margin of gena sharply angulate; gena with fine pale setulae. Subcranial cavity small to large.

Thorax: Presutural or sutural dorsocentral seta inconspicuous or absent; prescutellar acrostichal setae small (about 1/2–2/3 length of posterior dorsocentral seta), inserted close together (distance between about 1/2 that between either prescutellar and the posterior dorsocentral seta on the same side) and behind or aligned with intra-alar seta; notopleural setae near ventral margin, either bearing 2 or with a single notopleural seta, inserted near posterior angle; scutellum with 2 pairs of marginal setae. Foreleg usually normal, forefemur slender (swollen in *Stratiothyrea* de Meijere), foretibia not ended in a large spur.

Abdomen: Abdominal tergites 2–4 subequal in width, microtomentose, but more or less smooth. Male terminalia: Epandrium generally as an inverted U; cercus well developed, lunate to ovate, generally bearing some setulae; surstylus well developed (lacking a presurstylus), longitudinal, pointed or emarginate apically, articulated ventrally with epandrium or partially fused to epandrium, usually bearing setulae; subepandrial sclerite lacking; gonites (pre and post) either separate with a small pregonite near base of postgonite or pregonite fused with lateral arm of hypandrium and postgonite usually an elongate structure; aedeagus usually simple, wider basally, apex often somewhat pointed; phallapodeme in lateral view roughly triangular with a conspicuous keel, usually asymmetrical; ejaculatory apodeme present; hypandrium usually elongate, not pouchlike.

Key to Genera and Subgenera of the Tribe Gymnomyzini

1. Both anterior and posterior notopleural setae present 2
–. Anterior notopleural seta lacking, posterior seta present 7

2. Pseudopostocellar setae well developed, length subequal to inner vertical seta; arista with several short hairs along dorsum, none longer than basal aristal width .... ***Chaetomosillus*** Hendel
–. Pseudopostocellar setae either greatly reduced or lacking; arista bearing 3–8 longer hairs along dorsum, longest hairs longer than width of anterior ocellus 3

3. Anal lobe of wing almost straight .... ***Hoploaegis*** Cresson
–. Anal lobe of wing distinct, forming a rounded angle 4

4. Alula well developed, height greater than subcostal cell, and auriculate; face below antennal grooves evenly convex and completely transversely wrinkled to form series of depressions .... ***Cerometopum*** Cresson
–. Alula weakly developed, height less than subcostal cell; face usually with a mid facial prominence or if convex not wrinkled as above 5

5. Forefemur lacking any stout setae along ventral surface; a prescutellar acrostichal seta present or absent .... ***Trimerogastra*** Hendel
–. Forefemur with a stout seta along posteroventral surface toward apical 1/3; lacking prescutellar acrostichal setae (*Athyroglossa* Loew) 6

6. Mesonotal setulae in regular rows; forefemur without posteroventral, spinelike setulae; aristal rays relatively short, length of longest rays about 1/2 or less width of 1st flagellomere .... Subgenus ***Parathyroglossa*** Hendel

–. Mesonotal setulae in irregular rows; forefemur bearing 3–7, short, posteroventral, spinelike setulae; aristal rays relatively long, length of longest rays equal or greater than 1/2 width of 1st flagellomere .... Subgenus ***Athyroglossa*** Loew

7. Arista bearing 3–9 moderately long hairs along dorsum, length of hairs considerably greater than basal aristal width; alula short 8

–. Arista appearing essentially bare, any hairs present short, length less than basal aristal width; alula high, auriculate 11

8. Face in lateral view concave, lacking a median facial projection; lateral margin of abdomen creased .... ***Platygymnopa*** Wirth

–. Face in lateral view protuberant, with a median facial projection; lateral margin of abdomen rounded 9

9. Forefemur greatly swollen, width twice that of mid- and hindfemora, bearing a ventral keel-like ridge; halter knob whitish .... ***Stratiothyrea*** de Meijere

–. Forefemur at most slightly enlarged, not twice width of mid- and hindfemora, ventral surface not with a keel-like ridge 10

10. Knob of halter black; dorsal fronto-orbital seta well developed, lateroclinate; outer vertical seta present, well developed .... ***Trimerogastra*** Hendel

–. Knob of halter white or whitish; no fronto-orbital setae well developed, setulae proclinate; outer vertical seta lacking .... ***Gymnopiella*** Cresson

11. Forefemur unarmed, lacking row of stout setae along posteroventral surface at apical 1/4; outer vertical seta absent; mesonotum with several setae in oblique row between postalar seta and base of scutellum .... ***Placopsidella*** Kertész

–.. Forefemur bearing 5–10 stout setae along posteroventral surface at apical 1/3; inner and outer vertical setae present; mesonotum lacking setae between postalar seta and base of scutellum 12

12. Gena short, gena-to-eye ratio 0.20; parafacial narrow, less than width of anterior ocellus; wing generally faintly infuscate, light brown .... species related to “***Gymnopa” beckeri*** Cresson

–. Gena high, gena-to-eye ratio 0.45 or greater; parafacial moderately to very wide, width greater than that of anterior ocellus; wing generally appearing milky white 13

13. Face appearing spotted and pitted, pits with silvery gray microtomentum; anterior surface of midfemur rounded, bare of microtomentum, shiny; forefemur with posteroventral margin produced ventrally to a pointed ridge bearing setae .... ***Chlorichaeta*** Becker

–. Face microsculptured but either bare or microtomentum in vertical stripes, unspotted; midfemur with anterior surface flat, densely microtomentose, microtomentum silvery white; forefemur bearing row of stout setae along apical half of posteroventral margin, these not arising from a pointed ridge .... ***Mosillus*** Latreille

Trimerogastra **Hendel**

Trimerogastra Hendel, 1914: 110. Type species: *Trimerogastra cincta* Hendel, 1914, original designation. Hendel, 1934: 14 [compared with *Chaetomosillus*]. Cresson, 1925: 241 [discussion of status and subfamily]; 1945: 51–52 [review, synonymy]. Cogan & Wirth, 1977: 323–324 [Oriental catalog]. Mathis & Zatwarnicki, 1995: 142 [world catalog].

Tetramerogastra Hendel, 1914: 111. Type species: *Tetramerogastra fumipennis* Hendel, 1914, original designation. Cresson, 1945: 51 [synonymy].

Pseudopelina Miyagi, 1977: 64. Type species: *Pseudopelina setosa* Miyagi, 1977, original designation. Zatwarnicki, 1991: 296 [synonymy].

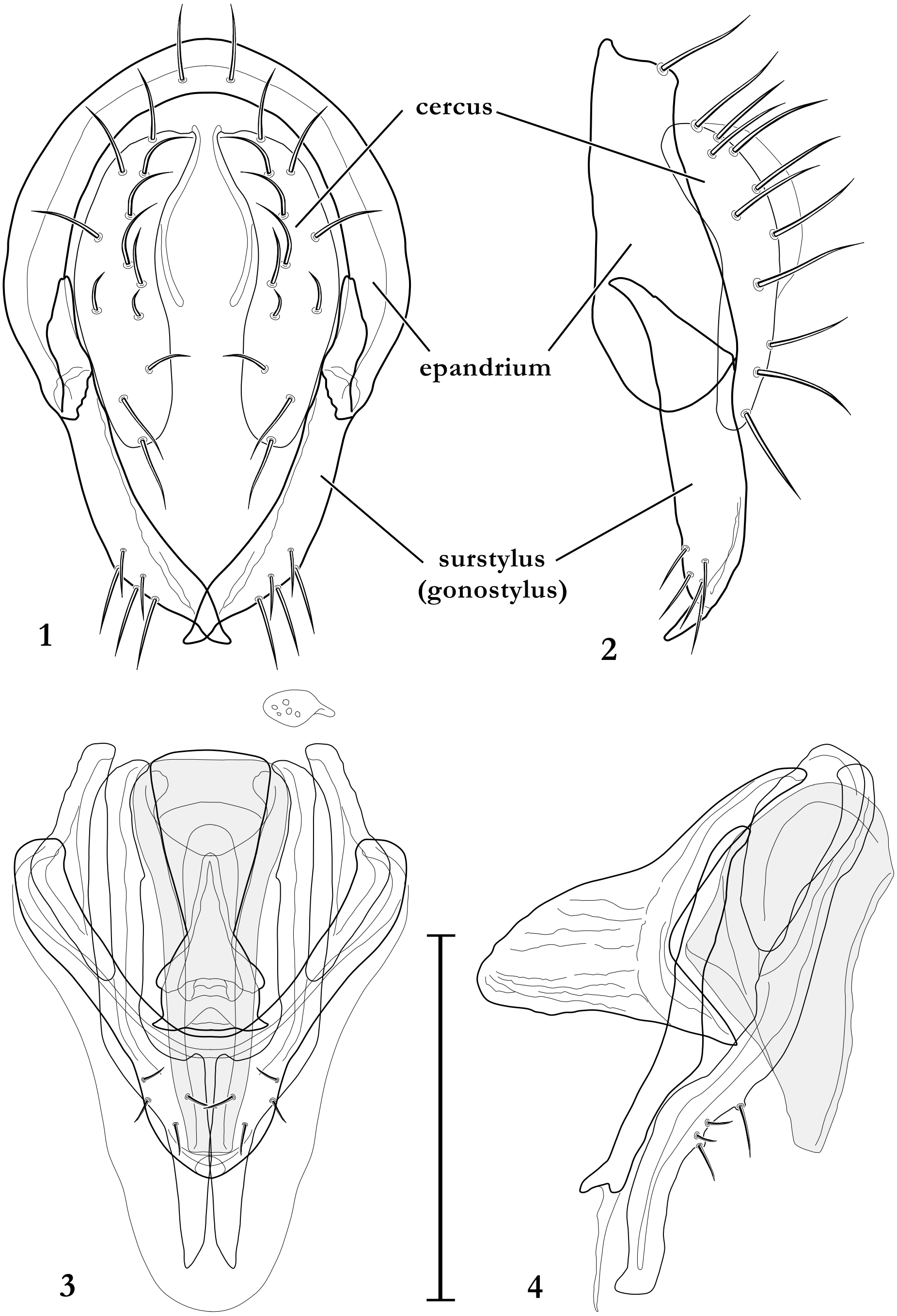
Diagnosis. *Trimerogastra* is distinguished from related genera of the tribe Gymnomyzini by the following combination of characters: Body mostly brownish microtomentose, especially on dorsum; setation generally well developed; posterior fronto-orbital seta lateroclinate or obliquely lateroclinate; middle facial conical protuberance moderately large; parafacial relatively narrow, lacking vertical row of furrows; gena moderately high to moderately low, about 1/4–1/3 height of eye; apical scutellar setae usually not arising from basal tubercles; wing faintly brownish hyaline; alula of wing narrow, bandlike; halter knob blackish brown to black; forefemur only slightly more swollen than mid- or hindfemora, lacking large ventral setae or keel-like process; midtibiae similar to fore- and hindtibiae, lacking anterodorsal surface flattened and invested with silvery white microtomentum; 2nd tergite lacking a median depression, linear to narrowly triangular; fifth tergite of males and to a lesser degree in females with median dorsal depression towards posterior margin; surstylus longitudinal, bearing setulae on distal portion; gonites very elongated, 1/3–1/2 longer than aedeagus.

Description. Small to moderately small shore flies, body length 1.35–2.30 mm, mostly black, many surfaces subshiny to shiny; dorsum, especially thorax, sometimes somewhat microtomentose, appearing subshiny to dull.

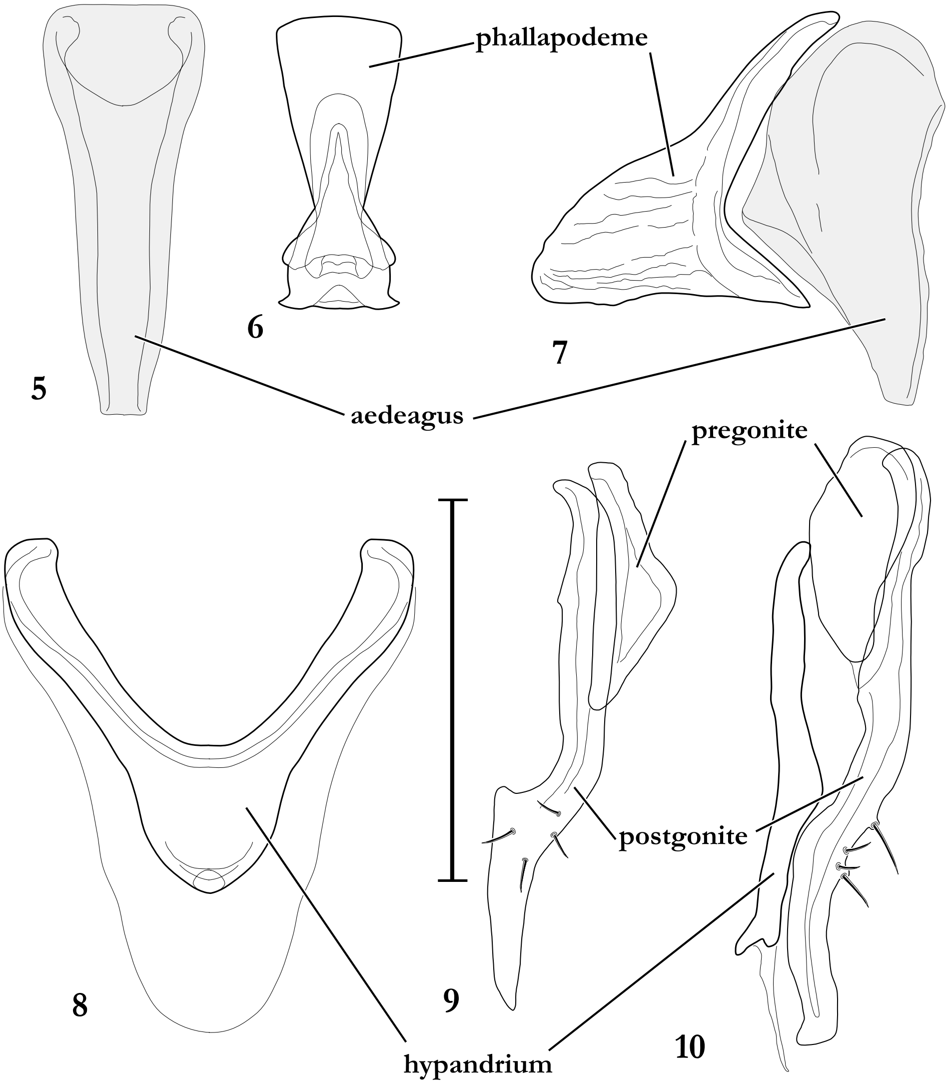
Head: Setation moderately well developed. Frons relatively wide, as wide or usually wider than long; ocelli arranged in isosceles triangle, distance between posterior ocelli greater than that between either posterior ocellus and anterior ocellus; ocellar setae well developed, generally proclinate, slightly divergent, inserted laterad of anterior ocellus; pseudopostocellar seta greatly reduced or lacking; 2 fronto-orbital setae, posterior fronto-orbital seta longer, obliquely lateroclinate to lateroclinate; anterior fronto-orbital setae proclinate; 1–3 smaller setulae between larger fronto-orbital setae, 1 setula usually larger, proclinate; both inner and outer vertical setae present, with outer seta slightly smaller than inner seta. Antenna normally developed; 1st flagellomere reddish brown, broadly rounded apically; arista comparatively long, longer than combined length of first 3 antennal segments, thickened basally, thereafter very gradually tapered to apex, bearing 3–8 dorsal hairs. Face with dorsal half vertically and shallowly carinate with distinct but shallow and wide antennal grooves; midfacial, conical protuberance moderately prominent; parafacial moderately narrow, becoming wider posteroventrally, width conspicuously greater than width of anterior ocellus; parafacial immediately adjacent to face lacking vertical row of horizontal grooves; gena generally bare and moderately high to moderately short, height about 1/4–1/3 eye height; posterior margin sharply angulate and marginate.

Thorax: Mesonotum black but densely invested with grayish brown to brown micro-tomentum, sometimes in longitudinal pattern. Only posteriormost dorsocentral seta and postalar seta well developed on scutum (a prescutellar acrostichal seta present in *T. cincta*); lacking row of prominent setae between postalar seta and base of scutellum; scutellum bearing well-developed apical setae, basal marginal setae moderately or weakly developed, these not arising from tubercles; notopleuron with 1 large posterior seta, anterior seta usually lacking, if present weakly developed; 2 anepisternal setae, ventral seta slightly larger, both at posterior margin; 1 katepisternal seta. Scutellum more or less rectangular or trapezoidal, posterior margin usually truncate, not pointed; disc densely setose; only apical scutellar setae well developed, these more or less approximate. Wing faintly brownish hyaline, basal color sometimes much darker; vein R_{2+3} moderately long, with length of costal section II about 1.5–2 × section III; vein CuA_1 not extended to wing margin; alula narrow, bandlike, alular marginal setulae much shorter than alular width. Halter knob blackish brown to black. Forefemur only slightly more swollen than mid- or hindfemora, lacking ventral processes or enlarged setae; midfemora with row of 6–8 stout setae on anterior surface; midtibia somewhat rounded, similar to fore- and hindtibiae, lacking flattened anterior surface that appears silvery white; femora and tibiae black, basitarsomere yellow, apical 1–2 tarsomeres usually blackish brown.

Abdomen: Generally blackish brown, thinly to moderately heavily microtomentose, microtomentum gray to grayish brown, lacking evident microsculpturing; anterior margin of tergites 2–4



Figures 1-4. Structures of the male terminalia of *Trimerogastra cincta* Hendel (Thailand. Sakla, Samut Prakan). **1**. Epandrium, cerci, and surstylus, posterior view; **2**. Same, lateral view; **3**. Aedeagus (shaded), phallapodeme, gonites, hypandrium, ejaculatory apodeme, ventral view; **4**. Same (not including ejaculatory apodeme), lateral view. Scale bar = 0.1 mm.



Figures. 5-10. Structures of the male terminalia of *Trimerogastra cincta* Hendel (Thailand. Sakla, Samut Prakan). **5**. Aedeagus, ventral view; **6**. Phallapodeme, ventral view; **7**. Aedeagus and phallapodeme, lateral view; **8**. Hypandrium, ventral view; **9**. Postgonite and pregonite, ventral view; **10**. Hypandrium, postgonite, and pregonite, lateral view. Scale bar = 0.1 mm.

with microtomentose bands, especially medially; tergites well sclerotized, continued laterally and ventrally, lateral margin rounded; 2nd tergite lacking median depression; sternites of male relatively weakly developed, usually as small sclerotized rectangular plates, 1st sternite of male oriented perpendicular to plane of body, sternites 2–4 parallel to plane of body; 5th sternite divided into 2 sternites, each longer than wide and oriented to form a V, with anterior vertex, sometimes fused at vertex; 5th tergite exposed but shorter than 4th, usually triangular or trapezoidal, with 2 dorsal pits toward posterior margin. Male terminalia: Epandrium in lateral view dorsoventrally elongate, wider ventrally, in posterior view widest at level of cerci; cercus ovate to semihemispherical, bearing short setae; surstylus simple, rodlike, 3–4 × longer than wide, bearing setulae apically; ejaculatory apodeme small, spatulate; aedeagus in ventral view wider basally, tapered to narrower apex, lateral margin even or sinuous, in lateral view wide basally, apical 1/2 tapered to blunt to acutely narrowed point; phallapodeme in lateral view asymmetrical, extended keel skewed to attachment with hypandrium; postgonite elongate, bearing setulae along posterior surface; pregonite a small, lateral sclerite near base of postgonite; hypandrium much longer than wide, narrow, linear.

Distribution. Australasian, Oriental, and eastern Palaearctic (Japan) Regions.

Natural history. Although one or two species of *Trimerogastra* occur inland in association with saltpans or in freshwater habitats (the undescribed species), most species are associated primarily with coastal mangrove or other brackish-water habitats where specimens can be relatively abundant. Nothing is known about the immature stages or life history of the genus.

Key to Species of *Trimerogastra* Hendel

1. Dorsal aristal rays 5–8. Vein R_{2+3} long, nearly straight, length of costal section II about twice section III .... ***fumipennis*** (Hendel)
– Dorsal aristal rays 3–5. Vein R_{2+3} short, shallowly arched, especially subapically, length of costal section II only slightly longer than section III... 2

2. Tergites, especially 3 and 4, uniformly sparsely microtomentose, lacking dense microtomentose fascia toward anterior half .... ***mcalpinei*** **n.sp.**
– Tergites, especially 3 and 4, either with fasciate pattern of dense microtomentose toward anterior 1/2, contrasted with sparsely microtomentose posterior half or uniformly thinly whitish microtomentose 3

3. Tergites 3–5 thinly and more or less uniformly whitish microtomentose, microtomentum toward anterior margin slightly denser but not distinctly fasciate. Gena moderately high, about 1/3 eye height; arista bearing 4–5 hairs, longest longer than height of 1st flagellomere. Scutellum rectangular, posterior margin wide, bluntly rounded, surface grossly sculptured .... ***hardyi*** **n. sp.**
– Tergites 3–4 with distinct fasciate pattern of microtomentum toward anterior margin of tergite. Gena relatively short, about 1/4 eye height; arista bearing 3–4 hairs, longest shorter than height of 1st flagellomere. Scutellum trapezoidal, posterior margin relatively narrow, surface similar to scutum 4

4. Gena moderately short, about 1/4 eye height; arista bearing 3–4 hairs, longest shorter than height of 1st flagellomere; prescutellar acrostichal seta present. Tergites 3–4 fasciate, anterior portion whitish gray microtomentose, posterior portion very sparsely brownish microtomentose; femora and tibiae essentially concolorous .... ***cincta*** Hendel
– Gena very short, about 1/8 eye height; arista bearing 4 hairs, longest at least equal to height of 1st flagellomere; prescutellar acrostichal seta lacking. Tergites 3–4 with microtomentum in small, separate, more lateral patches toward anterior margin; tibiae conspicuously lighter in color than femora .... ***Trimerogastra*** sp.

Trimerogastra cincta Hendel
(Figs. 1–10)

Trimerogastra cincta Hendel, 1914: 111. Cresson, 1925: 241 [discussion of status]; 1945: 51 [review]. Cogan & Wirth, 1977: 323 [Oriental catalog]. Mathis & Zatwarnicki, 1995: 142 [world catalog].

Diagnosis. This species is distinguished from congeners by the following combination of characters: Small shore flies, body length 1.35–1.90 mm.

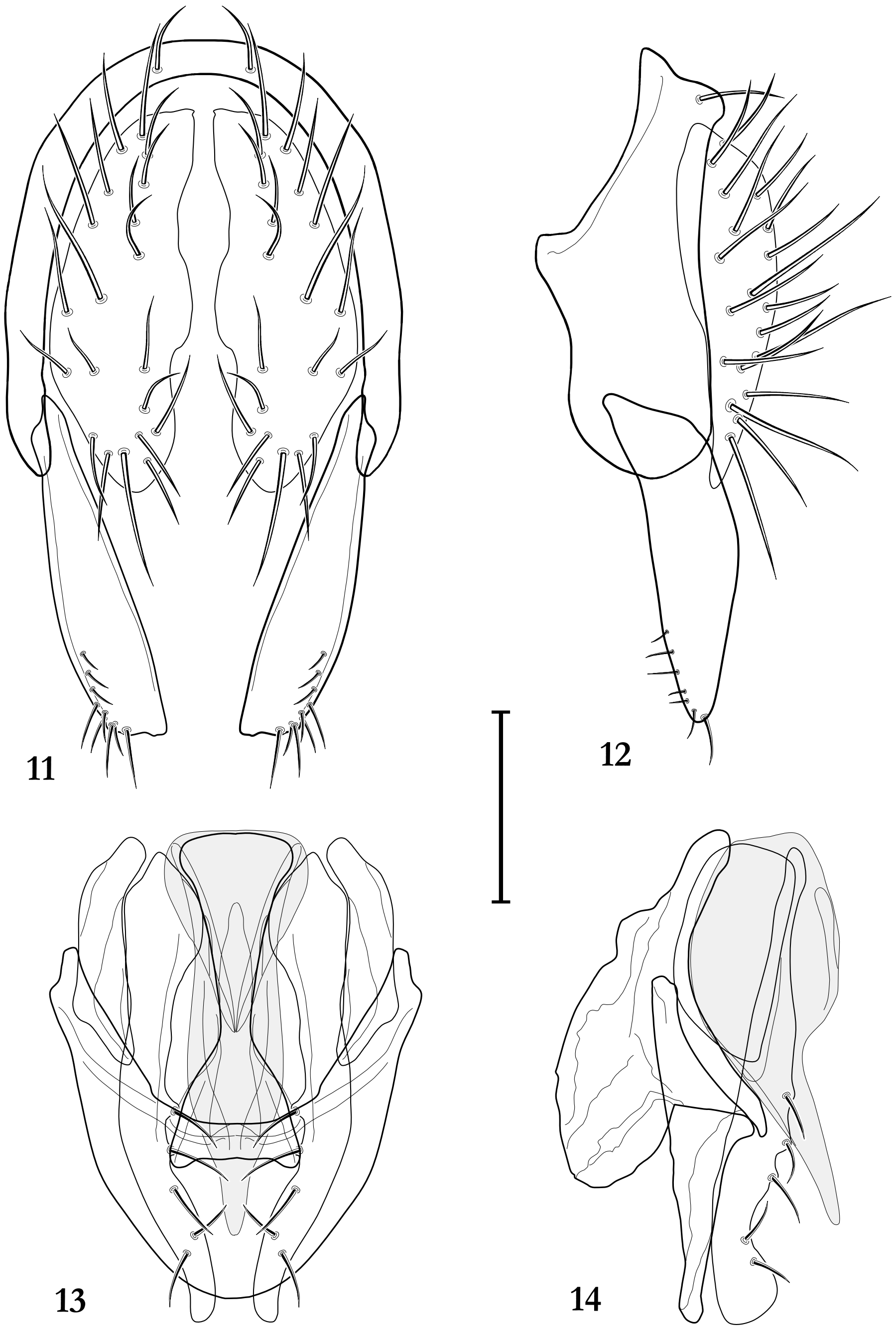
Head: Posterior fronto-orbital seta obliquely posterolateroclinate to lateroclinate, length conspicuously longer than anterior proclinate seta; distance between anterior and posterior seta greater than distance between posterior ocelli. Arista bearing 3–4, short hairs, longest hair shorter than height of 1st flagellomere. Gena relatively short, about 1/4 eye height and less than height of 1st flagellomere; gena-to-eye ratio 0.25–0.28.

Thorax: Prescutellar acrostichal seta present; scutellum broadly trapezoidal, wider than long, posterior margin relatively narrow, surface similar to scutum; apical setae long, length subequal to scutellar length. Vein R_{2+3} shallowly arched, especially subapically, moderately short; length of costal section II about 1.4 × longer than section III; costal vein ratio 0.70–0.71; M vein ratio 0.44–0.48. Femora and tibiae black, essentially concolorous with katepisternum.

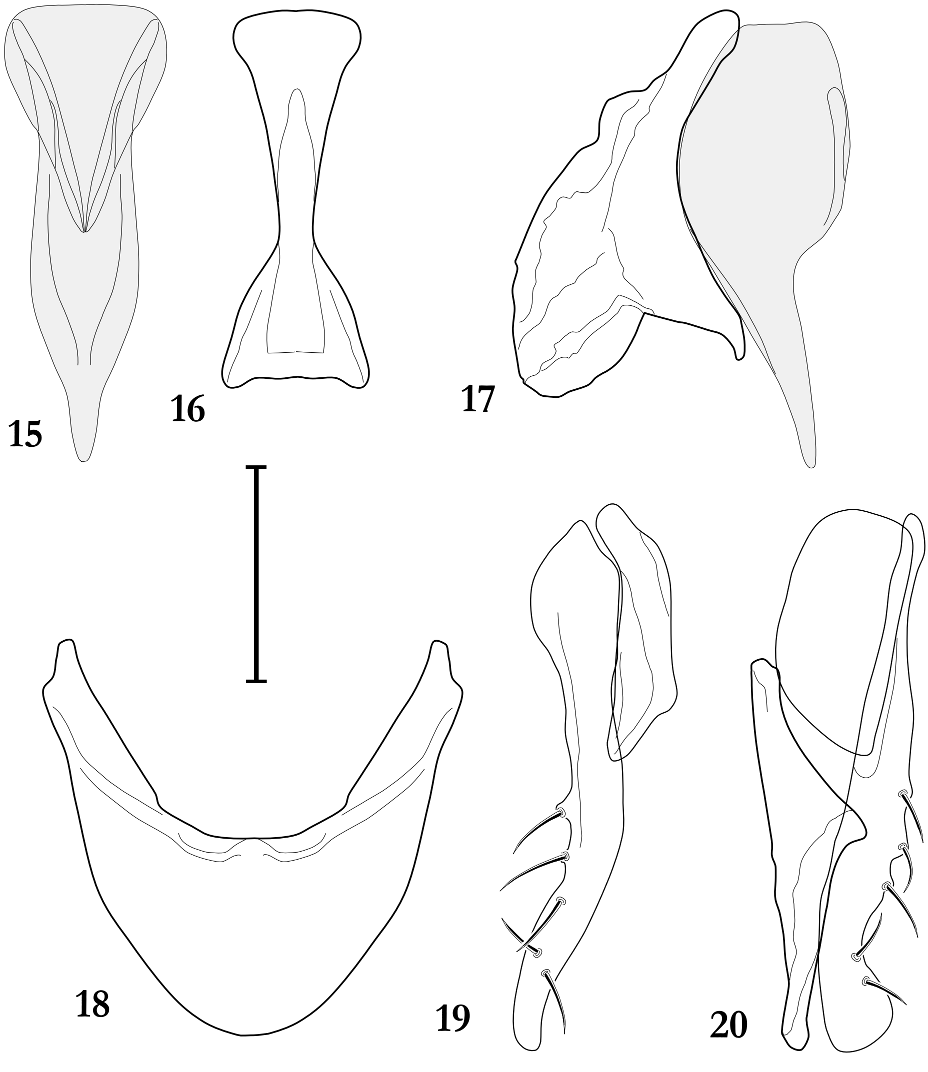
Abdomen: Tergites 3–4 fasciate, anterior portion whitish gray microtomentose, posterior portion very sparsely microtomentose. Male terminalia (Figs. 1–10): Epandrium in posterior view (Fig. 1) as an inverted U, rounded, in lateral view (Fig. 2) gradually becoming wider ventrally, ventral margin rounded; cercus in posterior view (Fig. 1) semihemispherical, slightly more sclerotized dorsomedially and with a dorsomedial, short projection, otherwise parallel sided, shallowly curved; surstylus in posterior view long and narrow, as long as height of epandrium, apical 1/3 turned medially, this portion bearing longer setulae, acutely pointed apically; aedeagus in ventral view (Figs. 3, 5; shaded) with base about twice width of apex, apex truncate, in lateral view (Figs. 4, 7) wide basally, apical half tapered to narrow and truncate apex; phallapodeme in lateral view (Figs. 4, 7) with extended keel asymmetrically triangular, rounded, projected erectly; postgonite in lateral view (Figs. 4, 10) elongate, narrow, step-curved medially, bearing 3–4 setulae at midlength, apex truncate, in ventral view (Figs. 3, 9) curved medially just beyond midlength, more sharply angulate medially; pregonite linearly triangular in ventral view (Figs. 3, 9), irregularly oval in lateral view (Figs. 4, 10); hypandrium in ventral view (Figs. 3, 8) V- to Y-shaped, with wide extended anteromedial process and narrow, posterolateral arms, in lateral view (Figs. 4, 10) elongate and narrow.

Type Material. The lectotype male, here designated to stabilize and make more universal the use of this name, is labeled "Anping Formosa [Taiwan] H. Sauter, VI. 1912 [Jun 1912]/TYPUS [pink]/*Trimerogastra* cincta H. det.Hendel [species name and "H." handwritten]/Eberswalde coll. DEI/LECTOTYPE ♂ *Trimerogastra* cincta Hendel By Mathis and Zatwarnicki [handwritten except for "LECTOTYPE" and "By"; black sub-border]." The lectotype is double mounted (minuten in a rectangular block of plastic foam), is in good condition (some scutellar setae are missing), and is deposited in the DEI. There are also 13 paralectotypes that are deposited in DEI (4♂, 3♀), ANSP (1♂, 1♀), and NMW (2♂, 2♀).

Other Specimens Examined. Oriental. **INDIA**. Tamil Nadu: Madras, Guindy, 17 Aug 1913, Fletcher (1♀; ANSP). **MALAYSIA**. Sedili kecil (mangrove), 11–12 Oct 2000, P. Grootaert (7♂, 5♀; KBIN, sample no. 20043-47). **SINGAPORE**. Changi (mangrove), 14 Aug 1976, D.H. Murphy (1♂; BMNH). **SRI LANKA**. Eastern Province. Batticaloa: Batticaloa, 2 May 1980, L. Jayawickrema, W. N. Mathis, T. Wijesinhe (7♂, 6♀; USNM); Panichchankeni, 2 May 1980, L. Jayawickrema, W. N. Mathis, T. Wijesinhe (1♂; USNM). Tricomalee: Mutur, 2 May 1980, L. Jayawickrema, W. N. Mathis, T. Wijesinhe (1♀; USNM). Southern Province. Hambantota: Bundala, 25 Apr 1980, L. Jayawickrema, W. N. Mathis, T. Wijesinhe (3♂, 2♀; USNM); Kirinda, 25 Apr 1980, L. Jayawickrema, W. N. Mathis, T. Wijesinhe (1♂, 1♀; USNM). **TAIWAN**. Takao, 2 May 1907, H. Sauter (1♂; ANSP). **THAILAND**. Hat Chandamri, Ranong (beach), 9 May 1998, P. Grootaert (4♂, 1♀; KBIN, sample no. 98038-43). Kanchanadit, Surat Thani (river bed, pools), 12 May 1998, P. Grootaert (1♂; KBIN, sample no. 98051). Laem Son, Ranong (mangrove), 10 May 1998, P. Grootaert (5♂, 1♀; KBIN, sample no. 98046). Pak Bara, Satun (mangrove), 28 Oct 1997, P. Grootaert (4♂, 2♀; KBIN, sample no. 97132). Prachuap Khiri Khan: Prachuap Khiri Khan, 2 Apr 1996, P. Grootaert (1♂, 2♀; KBIN, sample no. 96006).



Figures 11–14. Structures of the male terminalia of *Trimerogastra fumipennis* Hendel (Taiwan. Tainan). **11**. Epandrium, cerci, and surstylus, posterior view; **12.** Same, lateral view; **13.** Aedeagus (shaded), phallapodeme, gonites, and hypandrium, ventral view; **14**. Same, lateral view. Scale bar = 0.1 mm.



Figures. 15-20. Structures of the male terminalia of *Trimerogastra fumipennis* Hendel (Taiwan. Tainan). **15**. Aedeagus, ventral view; **16**. Phallapodeme, ventral view; **17**. Aedeagus and phallapodeme, lateral view; **18**. Hypandrium, ventral view; **19**. Postgonite and pregonite, ventral view; **20**. Hypandrium, postgonite, and pregonite, lateral view. Scale bar = 0.1 mm.

Sakla, Samut Prakan (mangrove), 20 May 1998, P. Grootaert (60♂, 23♀; KBIN, sample no. 98060). Sam Roi Yot, Prachuap Khiri Khan (rocks on beach, mangrove), 2 Apr 1996, P. Grootaert (3♂, 2♀; KBIN, sample no. 96001-02). Su-Saan Hawy, Krabi (sandy beach), 24 Oct 1997, P. Grootaert (1♂; KBIN, sample no. 97111). Takua Pa, Phang-Nga (river, estuary), 8 May 1998, P. Grootaert (1♀; KBIN, sample no. 98031). Tha Po, Surat Thani (mangrove creek), 12 May 1998, P. Grootaert (28♂, 7♀; KBIN, sample no. 98052).

Distribution. Oriental: India (Tamil Nadu), Malaysia, Singapore, Sri Lanka, Taiwan, Thailand.

Remarks. Although originally described from specimens collected in Taiwan, this species is much more widespread, occurring throughout much of the Oriental Region along maritime coasts.

***Trimerogastra fumipennis* (Hendel)**

(Figs. 11–20)

Tetramerogastra fumipennis Hendel, 1914: 111.

Trimerogastra fumipennis. Cresson, 1945: 51 [generic combination]. Cogan & Wirth, 1977: 324 [Oriental catalog]. Mathis & Zatwarnicki, 1995: 142 [world catalog].

Pseudopelina setosa Miyagi, 1977: 65. **New Synonym**.

Trimerogastra setosa. Zatwarnicki, 1991: 297 [generic combination]. Mathis & Zatwarnicki, 1995: 142 [world catalog].

Diagnosis. This species is distinguished from congeners by the following combination of characters: Small to moderately small shore flies, body length 1.90–2.25 mm.

Head: Posterior fronto-orbital seta lateroclinate, long, over twice length of anterior, proclinate seta; distance between anterior and posterior setae less than distance between posterior ocelli. Arista bearing 5–8 short, dorsal hairs, none greater in length that height of 1st flagellomere. Gena moderately high to high, about 1/3 eye height and greater than height of 1st flagellomere; gena-to-eye ratio 0.36.

Thorax: Prescutellar acrostichal seta absent; scutellum trapezoidal, length subequal to width, disc similar to scutum, apical setae as long as scutellar length. Vein R_{2+3} nearly straight, long, only apex sometimes shallowly curved; length of costal section II about twice section III; costal vein ratio 0.47–0.50; M vein ratio 0.54–0.60. Femora and tibiae yellowish brown, tawny, distinctly lighter in color than katepisternum to blackish brown.

Abdomen: Tergite 2 generally with fine, lacteous microtomentum, tergites 3–4 with denser lacteous microtomentum anterolaterally, otherwise sparsely microtomentose except for sparsely microtomentose lateral margins. Male terminalia (Figs. 11–20): Epandrium in posterior view (Fig. 11) as an inverted U, rounded, in lateral view (Fig. 12) widest at midlength, ventral half almost parallel sided, ventral margin broadly rounded; cercus in posterior view (Fig. 11) semihemispherical, medial margin irregular, lateral margin more evenly curved; surstylus in posterior view long and narrow, nearly straight, as long as height of epandrium, gradually becoming wider ventrally, apical 1/3 bearing setulae; aedeagus in ventral view (Figs. 14–15, 17; shaded) with base about twice width as apex, apex narrowly pointed, lateral margins sinuous, in lateral view (Figs. 14, 17) wide basally, apical half tapered to narrowly formed apex; phallapodeme in lateral view (Figs. 14, 17) with extended keel asymmetrically triangular, rounded, inclined or skewed toward end that attaches with hypandrium; postgonite in lateral view (Figs. 14, 20) elongate, with shallowly angulate at midlength, narrow, apex rounded, bearing 3–4 setulae along posterior margin, in ventral view (Figs. 13, 19) tapered evenly to rounded apex, curved slightly along length; pregonite in ventral view (Figs. 13, 19) about 1/2 length of postgonite, slightly tapered at apices, generally linear, in lateral view (Figs. 14, 20) irregularly rectangular with apical margin slightly extended and pointed; hypandrium in ventral view broadly V-shaped with wide base and narrow, posteriorly directed arms, in lateral view (Figs. 14, 20) elongate and narrow, tapered to nearly digitiform apex.

Type Material. The lectotype male of *Tetramerogastra fumipennis,* here designated to stabilize and make more universal the use of this name, is labeled "Anping Formosa [Taiwan] H. Sauter, V. 1912 [May 1912]/TYPUS [pink]/Tetramerogastra fumipennis H. det. Hendel [species name and "H." handwritten]/ Eberswalde coll. DEI/LECTOTYPE ♂ Tetramerogastra fumipennis Hendel By Mathis and Zatwarnicki [handwritten except for "LECTOTYPE" and "By"; black sub-border]." The lectotype is double mounted (minuten in a rectangular block of plastic foam), is in fair condition (head missing), and is deposited in the DEI. Two male paralectotypes (1♂; DEI (head missing), 1♂; NMW) bear the same label data as the lectotype.

The holotype male of *Pseudopelina setosa* Miyagi is labeled "Iriomote[-jima] 16–IV–1962 [16 Apr 1962]/RYUKYU IS. I. Miyagi/-type Pseudopelina setosa I. Miyagi [red; all except "-type" handwritten]." The holotype is double mounted (minuten in a narrow, rectangular card), is in good condition (left wing largely missing, only base present, some setae missing or misoriented), and is deposited in the HUS.

Other Specimens Examined. **TAIWAN**. Kanshizei, H. Sauter (1♀; DEI). Tainan, Nov 1909, H. Sauter (1♀; ANSP).

Distribution. Oriental: Japan (Ryukyu Islands), Taiwan. Palearctic: Japan (Kyushu).

Remarks. We propose the synonymy of *Pseudopelina setosa* with *T. fumipennis* after direct comparison of the respective holotype and lectotype specimens. Although there is very slight variation in structures of the male terminalia, we are confident that the specimens are conspecific.

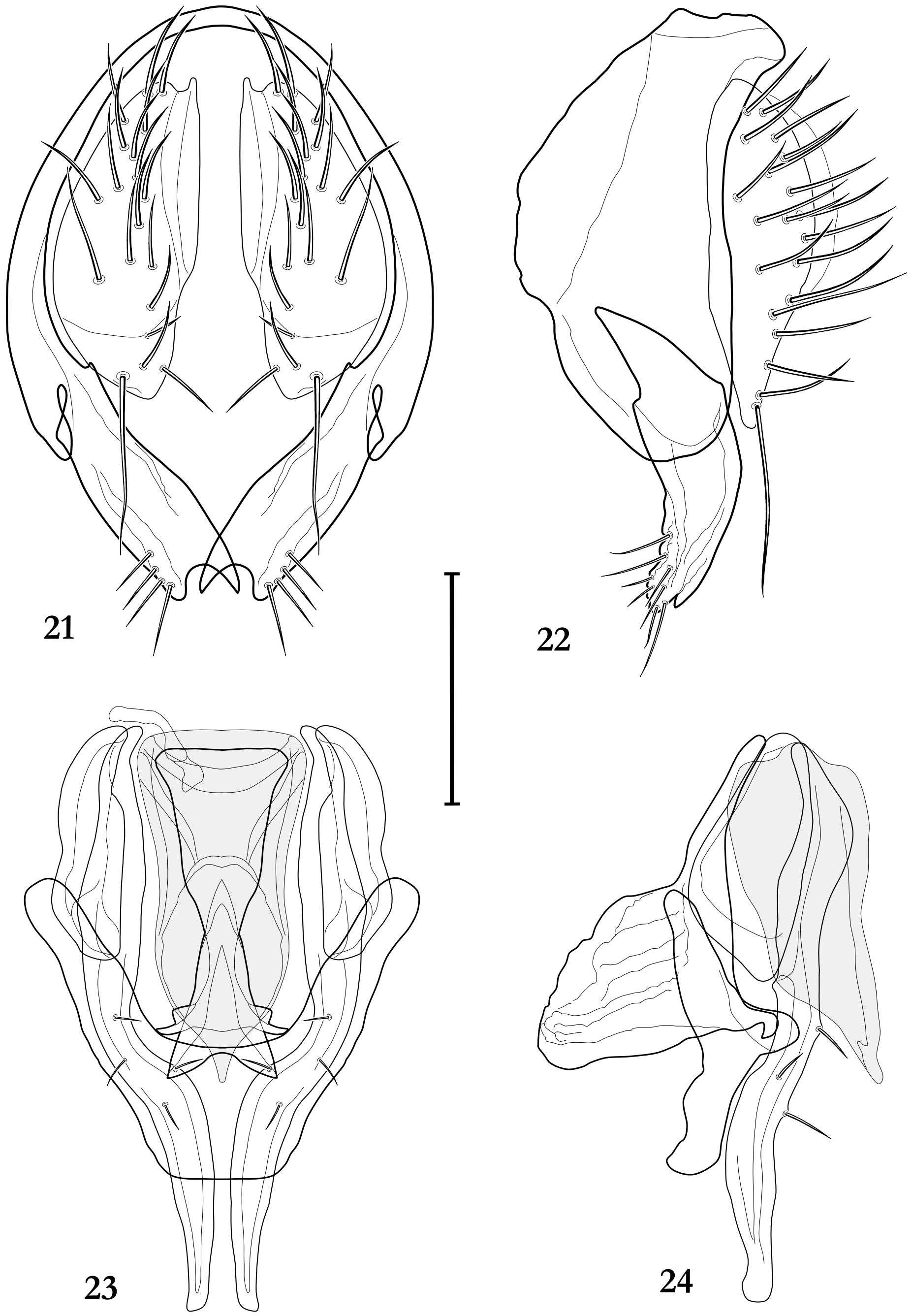
Trimerogastra hardyi Mathis & Zatwarnicki, **new species**
(Figs. 21–30)

Diagnosis. This species is distinguished from congeners by the following combination of characters: Small to moderately small shore flies, body length 1.45–2.30 mm.

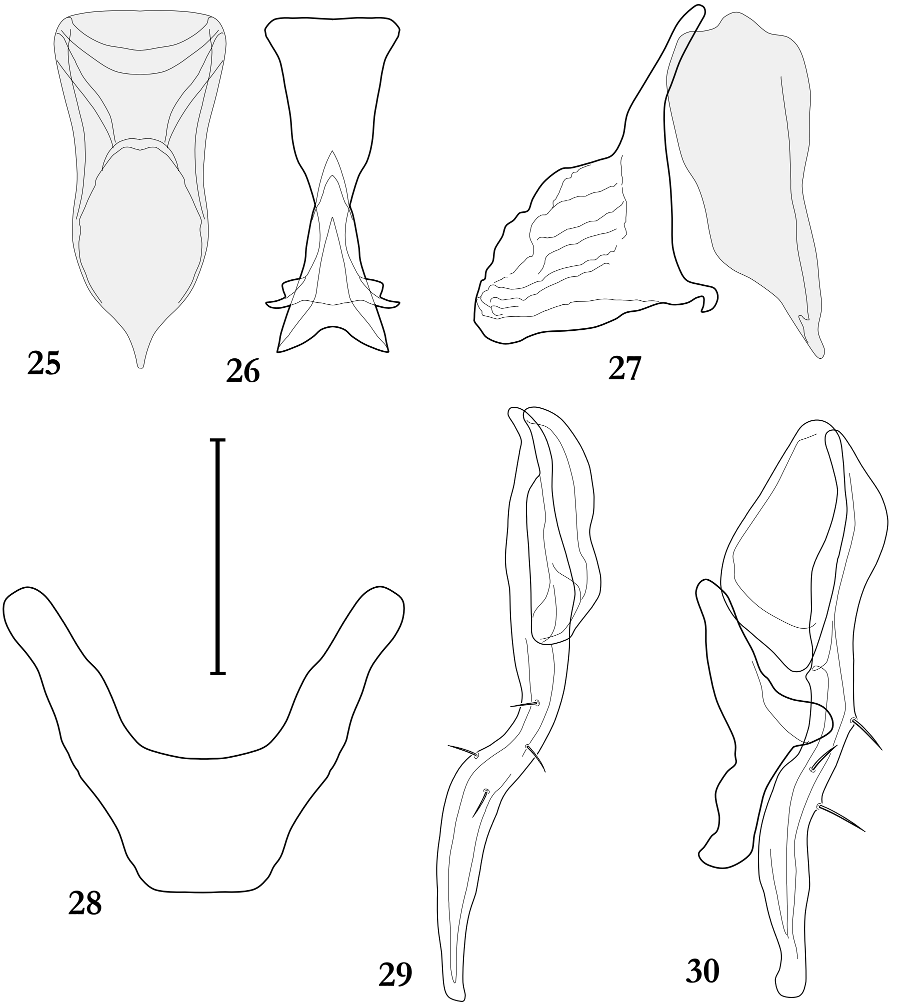
Head: Posterior fronto-orbital seta longer than anterior seta, lateroclinate; distance between anterior and posterior setae about equal to that between posterior ocelli. Arista bearing 4–5 long hairs, longest hair greater than height of 1st flagellomere. Gena moderately high, about 1/4–1/3 eye height, conspicuously higher than height of 1st flagellomere; gena-to-eye ratio 0.25–0.31.

Thorax: Prescutellar acrostichal seta absent; scutellum subquadrate, posterior margin wide, shallowly and bluntly rounded, disc grossly sculptured; apical setae conspicuously shorter than scutellar length. Costal vein ratio 0.90–0.95; vein R_{2+3} shallowly arched, especially subapically, short, making length of 2nd costal section only slightly longer than 3rd section; M vein ratio 0.55–0.64. Femora and tibiae black, essentially concolorous with katepisternum.

Abdomen: Tergites 3–4 generally invested with whitish gray microtomentum, contrasted with sparsely microtomentose posterior half. Male terminalia (Figs. 21–30): Epandrium in posterior view (Fig. 21) as a rounded, inverted U, in lateral view (Fig. 22) widest at midlength, ventral half wide, slightly tapered (almost parallel sided), ventral margin broadly rounded; cercus in posterior view (Fig. 21) semihemispherical, medial margin irregular, lateral margin more evenly curved; surstylus in posterior view long and narrow, nearly straight, almost as long as height of epandrium, gradually becoming wider ventrally, apical 1/3 bearing setulae laterally, apex concave, forming a medial point; aedeagus in ventral view (Figs. 23, 25; shaded) somewhat hour-glass shaped, with truncate base and narrowly pointed apex, and slightly concave laterally, in lateral view (Figs. 24, 27) wide basally, apical half tapered to narrowly formed apex; phallapodeme in lateral view (Figs. 24, 27) with extended keel asymmetrically triangular to trapezoidal, rounded, inclined or skewed toward end that attaches with hypandrium; postgonite in lateral view (Figs. 24, 30) elongate, shallowly sinuous, bearing setulae near midlength, in ventral view (Figs. 23, 29) tapered evenly to rounded apex, with an elbow curve at midlength; pregonite in ventral view (Figs. 23, 29) about 1/3 length of postgonite, slightly tapered at apices, generally linear, in lateral view (Figs. 24, 30) irregularly rectangular with apical margin slightly extended and bluntly pointed; hypandrium broadly V-shaped in ventral view (Figs. 23, 28), in lateral view (Figs. 24, 30) elongate but with a short process at midlength, apex bluntly rounded.



Figures. 21–24. Structures of the male terminalia of *Trimerogastra hardyi* n. sp. (Australia. Queensland: Cairns). **21**. Epandrium, cerci, and surstylus, posterior view; **22**. Same, lateral view; **23**. Aedeagus (shaded), phallapodeme, gonites, and hypandrium, ventral view; **24**. Same, lateral view. Scale bar = 0.1 mm.



Figures. 25–30. Structures of the male terminalia of *Trimerogastra hardyi* n. sp. (Australia. Queensland: Cairns). **25**. Aedeagus, ventral view; **26**. Phallapodeme, ventral view; **27**. Aedeagus and phallapodeme, lateral view; **28**. Hypandrium, ventral view; **29**. Postgonite and pregonite, ventral view; **30**. Hypandrium, postgonite, and pregonite, lateral view. Scale bar = 0.1 mm.

Type Material. The holotype male is labeled “AUSTRALIA: [Queensland] Cairns[,] 18–21 Dec 1976[,] Gary F. Hevel/HOLOTYPE Trimerogastra hardyi W.N. Mathis & T. Zatwarnicki USNM [red; USNM crossed out; species name, gender symbol, and “& T. Zatwarnicki” handwritten].” The holotype is double mounted (minuten in a block of polyporus), is in good condition (one apical scutellar seta missing), and is deposited in the AMS. Four paratypes (2♂, 2♀; USNM) bear the same label data as the holotype. Other paratypes are as follows: PAPUA NEW GUINEA. Central: Lea Lea, 23 Feb 1986, J. W. Ismay (1♂, 3♀; USNM).

Distribution. Australasian/Oceanian: Australia (Queensland), Papua New Guinea (Central).

Etymology. The species epithet, *hardyi,* is a Latin patronym to honor and recognize the voluminous contributions of our friend, D. Elmo Hardy, to dipterology, including his personal encouragement of us in our various studies of true flies.

Trimerogastra mcalpinei Mathis & Zatwarnicki, **new species**

(Figs. 31–40)

Diagnosis. This species is distinguished from congeners by the following combination of characters: Small to moderately small shore flies, body length 1.70–2.10 mm.

Head: Posterior fronto-orbital seta conspicuously longer than proclinate, anterior seta, lateroclinate; distance between anterior seta and posterior seta about equal to that between posterior ocelli. Arista bearing 4–5 hairs, longest hairs subequal to height of 1st flagellomere. Gena moderately high, about 1/4 eye height and greater than height of 1st flagellomere; gena-to-eye ratio 0.25–0.27.

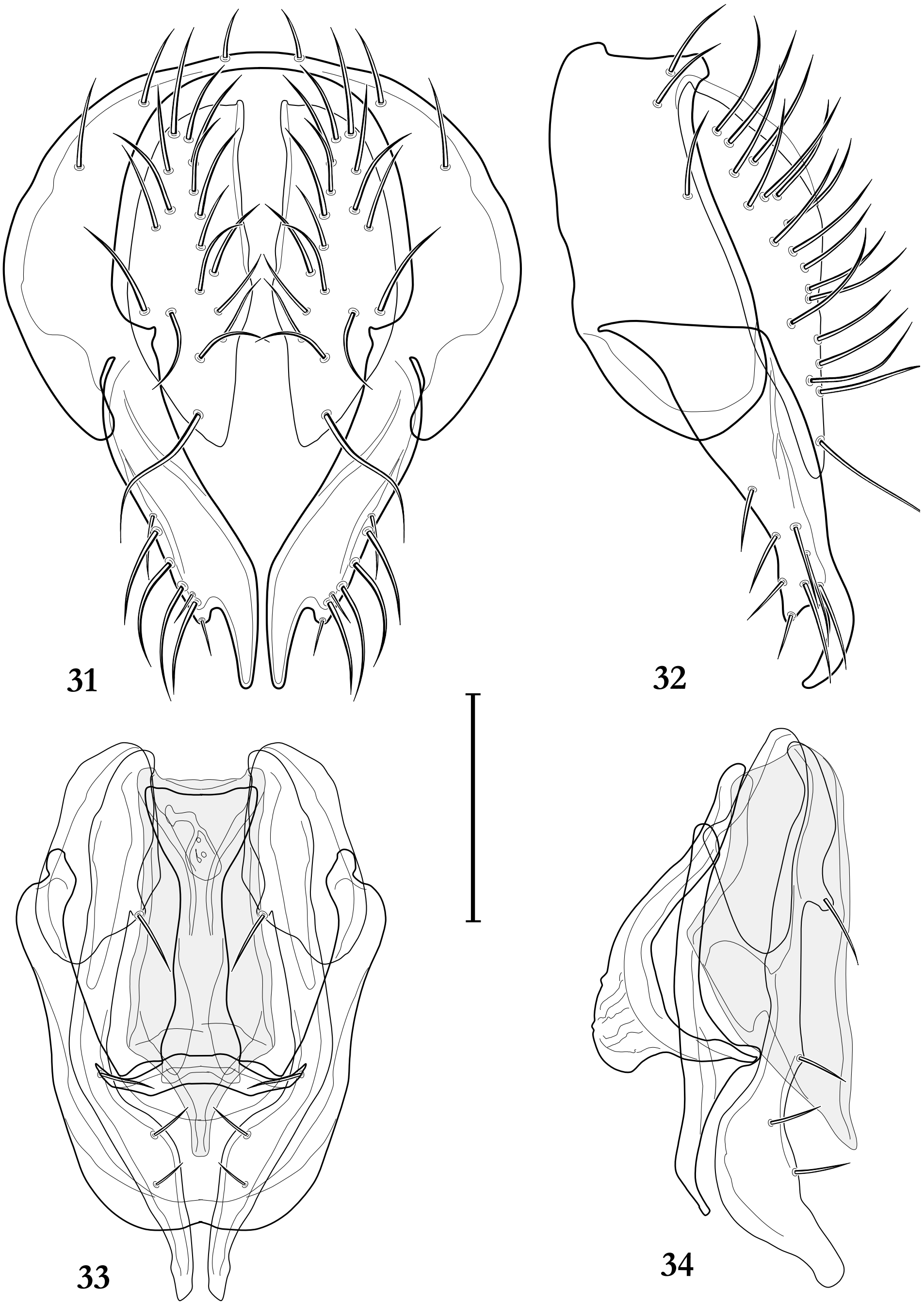
Thorax: Prescutellar acrostichal seta absent; scutellum trapezoidal, length subequal to width, disc similar to scutum, apical setae as long as scutellar length. Costal vein ratio 0.67–0.76; vein R_{2+3} moderately straight and long; costal section II about 1.5 × section III; M vein ratio 0.50–0.53.

Abdomen: Tergites, especially 3 and 4, uniformly sparsely microtomentose, lacking dense, microtomentose fascia toward anterior half. Male terminalia (Figs. 31–40): Epandrium in posterior view (Fig. 31) as a broadly rounded, inverted U, in lateral view (Fig. 32) essentially parallel sided with broadly rounded ventral margin; cercus in posterior view (Fig. 31) semihemispherical, medial margin irregular, lateral margin more evenly curved; surstylus in posterior view long and narrow, nearly straight, almost as long as height of epandrium, gradually becoming wider ventrally, apical 1/2 bearing setulae laterally, apex narrowly concave, forming an extended, medial point, apex sickle shaped in lateral view (Fig. 32); aedeagus in ventral view (Figs. 33, 35; shaded) with basal 2/3 rectangular with truncate base and apical 1/3 tapered to narrow point, in lateral view (Figs. 34, 37) moderately wide basally, becoming wider at midlength, thereafter tapered to narrowly formed apex; phallapodeme in lateral view (Figs. 34, 37) relatively narrow with short extended keel asymmetrically and shallowly trapezoidal, rounded, inclined or skewed toward end that attaches with hypandrium; postgonite in lateral view (Figs. 34, 40) elongate, shallowly sinuous, with a subbasal papilla that bears a setula, becoming widest subapically, bearing setulae near midlength, in ventral view (Figs. 33, 39) tapered nearly parallel sided, with sinuous medial margin and more evenly curved lateral margin; pregonite in ventral view (Figs. 33, 39) about 1/3 length of postgonite, irregularly oval in both ventral (Figs. 33, 39) and lateral (Figs. 34, 40) views; hypandrium broadly U-shaped in ventral view (Figs. 33, 38) with wide basal portion and thinner, posteriorly directed arms, in lateral view (Figs. 34, 40) elongate but with a short process at midlength, apex narrow and narrowly truncate.

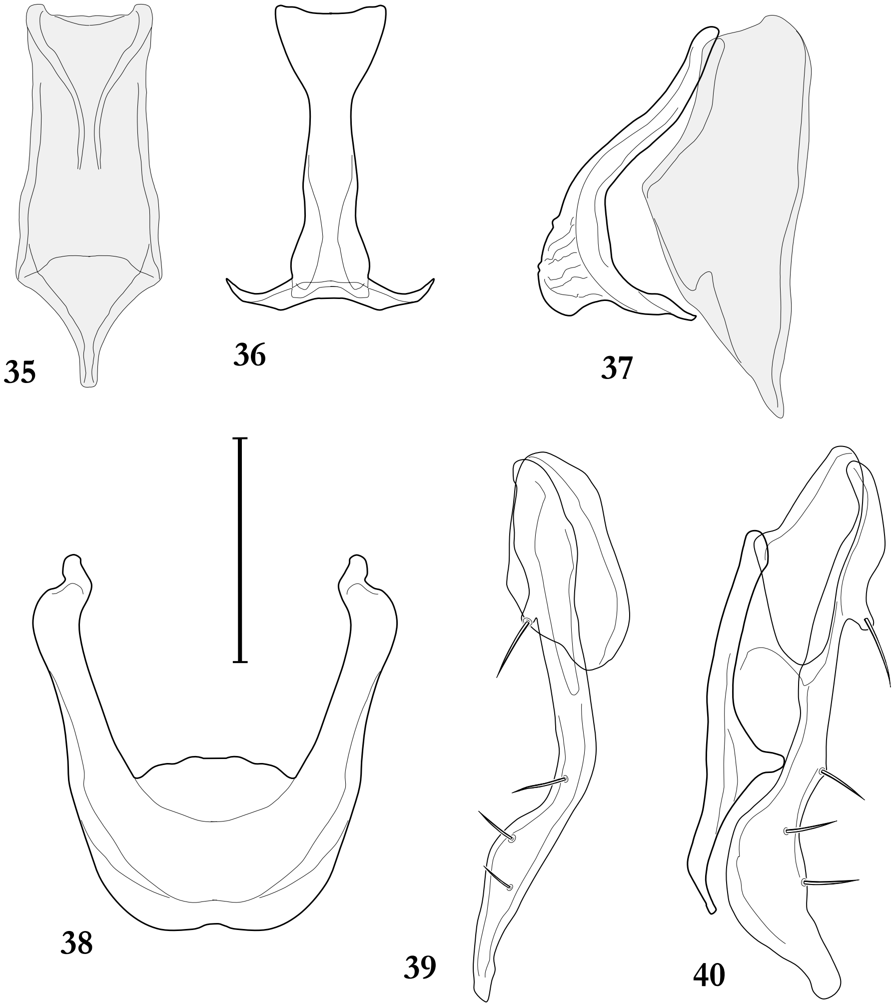
Type Material. The holotype male is labeled “AUSTRALIA. N[ew].S[outh].W[ales]. Cornulla (34º2.1'S, 151º9.1'E), 22 Feb 1998, W. N. Mathis/USNM ENT 00084102 [plastic bar code label]/HOLOTYPE Trimerogastra mcalpinei W.N. Mathis & T. Zatwarnicki USNM [red; USNM crossed out; species name, gender symbol, and “& T. Zatwarnicki” handwritten].” The holotype is double mounted (minuten in a block of plastic), is in good condition (some setae not aligned correctly), and is deposited in the AMS. A female paratype (USNM) has the same label data as the holotype. Other paratypes are as follows: AUSTRALIA. New South Wales. Careel Bay, Avalon (mangrove), 15 Dec–14 Mar 1953, 1964, D.K. McAlpine (1♂ (head missing), 1♀; AMS, USNM). Queensland: Yorkey’s Knob (16º48.1'S, 145º43.1'E; mangrove), 26 Sep 2002, D. and W.N. Mathis (1♀; USNM).

Other Specimens Examined. **PAPUA NEW GUINEA**. Central: Lea Lea (saltpans), 23 Feb 1986, J.W. Ismay (1♀; USNM).

Distribution. Australia (New South Wales, Queensland), Papua New Guinea (Central).



Figures. 31–34. Structures of the male terminalia of *Trimerogastra mcalpinei* n. sp. (Australia. New South Wales: Cornulla). **31**. Epandrium, cerci, and surstylus, posterior view; **32**. Same, lateral view; **33**. Aedeagus (shaded), phallapodeme, gonites, and hypandrium, ventral view; **34**. Same, lateral view. Scale bar = 0.1 mm.



Figures 35–40. Structures of the male terminalia of *Trimerogastra mcalpinei* n. sp. (Australia. New South Wales: Cornulla). **35**. Aedeagus, ventral view; **36**. Phallapodeme, ventral view; **37**. Aedeagus and phallapodeme, lateral view; **38**. Hypandrium, ventral view; **39**. Postgonite and pregonite, ventral view; **40**. Hypandrium, postgonite, and pregonite, lateral view. Scale bar = 0.1 mm.

Etymology. The species epithet, *mcalpinei,* is a Latinized, genitive patronym to honor Dr. David K. McAlpine, one of the collectors of the type series.

***Trimerogastra* sp.**

Diagnosis. This species is distinguished from congeners by the following combination of characters: Small shore flies, body length 1.50–1.60 mm.

Head: Posterior fronto-orbital seta reclinate, comparatively short, subequal to anterior, proclinate seta; distance between anterior and posterior setae relatively short, less than that between posterior ocelli. Arista with 4 long hairs, length of longest (basal) hairs greater than height of 1st flagellomere. Gena short, height less than height of 1st flagellomere; gena-to-eye ratio 0.14–0.15.

Thorax: Prescutellar acrostichal seta absent; scutellum trapezoidal to almost triangular, lateral margins very shallowly arched, posterior margin very narrow, truncate, disc moderately setose, apical setae with length slightly less than scutellar length. Costal section II only slightly longer than section III; costal vein ratio 0.89–0.92; M vein ratio 0.38–0.40.

Abdomen: Tergite 2 with sparsely, grayish brown microtomentum; tergites 3–4 with dense, transverse patches of whitish microtomentum anterolaterally, lateral margins thinly microtomentose, subshiny to shiny. Males unknown.

Specimens Examined. **AUSTRALIA**. Queensland: Iron Range (mushroom bait; rain forest), 4 Nov 1975, I. A. Bock, P. A. Parsons (1♀; USNM). **PAPUA NEW GUINEA**. Central: Brown River Bridge (5 km NW; forest), 18 May 1986, J. W. Ismay (1♀; USNM).

Distribution. Australasian/Oceanian. Australia (Queensland), Papua New Guinea (Central).

Remarks. We are not naming this species here because it is presently represented only by the two females noted above and we would prefer to have a male to characterize the species properly.

Acknowledgments

We gratefully acknowledge the assistance and cooperation of many organizations and individuals who contributed to the field work and production of this paper. To David A. Grimaldi (AMNH), Jon K. Gelhaus and Jason D. Weintraub (ANSP), John E. Chainey (BMNH), Joachim Ziegler (DEI), M. Suwa and Ichiro Miyagi (HUS), Patrick Grootaert (KBIN), Ruth Contreras-Lichtenberg (NMW) and their institutions, who loaned specimens, we express our sincere thanks. We acknowledge with grateful thanks the long-term fellowship at KBIN that was provided to T. Zatwarnicki during the years 2000–2001 by the Belgian Office for Scientific, Technical and Cultural Affairs.

For reviewing a draft of this paper we thank Allen L. Norrbom and Stephen D. Gaimari. We are also grateful to Helmut Hollmann for granting financial support for the field work on Australia and at museums in Europe.

Field work in Australia was expedited by the able and pleasant assistance of Daniel J. Bickel, David K. McAlpine, Dianne Mathis, and Gregory W. Courtney.

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Chromosomal Phylogenies and Population Genetics of the Picture-Winged Hawaiian Drosophilids: Impact on Evolutionary Biology

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Abstract

Using a single species as a standard, the banding orders of the 6 giant chromosomes of each of 107 species of large Hawaiian drosophilids have been determined. Most banding orders vary due to naturally occurring inversions. The data on inversion sharing between species yields a robust genetically-based phylogeny for these species on all of the high Hawaiian islands. Species on the newer islands can be traced chromosomally to 6 putative ancestral forms on Kaua‘i. Population genetic studies of selected species reveals abundant intraspecific genetic variation involving female choice from among genetically variable males. The general value of these studies to some major concepts of evolutionary biology is discussed.

Introduction

About 40 years ago, a major project to study the evolutionary biology of the endemic Hawaiian Drosophilidae was launched by D. Elmo Hardy of the University of Hawaii and Wilson S. Stone of the University of Texas. The grant proposal approved by National Institutes of Health at the time stressed a multi-disciplinary approach. Accordingly, the principals were able to invite participation from a diverse set of biologists already having professional experience in various aspects of ecology, entomology, ethology, genetics, physiology and systematics. Following the tragic death of Stone at the height of his career and only a few years into the project, its realization fell on the shoulders of Hardy, who continued over many years to facilitate the project. He provided both basic systematics and field guidance, without which the work to understand the evolution of this extraordinary fauna would have been seriously hampered.

The first year of the project was 1963. By noteworthy coincidence, this was the same year that a brief paper by J. Tuzo Wilson, a Canadian geologist, appeared in the *Canadian Journal of Science*. Wilson proposed the stunning theory that the Hawaiian Islands are the sub-aerial tips of great volcanoes that have been formed in a strictly successive manner over a localized “hot-spot” under the moving Pacific tectonic plate. As the plate has moved slowly north and later northwestward, each new volcano was formed at the current southeast end of the archipelago.

Since Wilson’s paper, data have accumulated that strongly support this theory (Clague & Dalrymple, 1987). Furthermore, the new data indicate that the Emperor Seamounts, a line of submerged extinct volcanoes dating back about 80 million years, have a similar but ancient origin. From this perspective, the present high islands are very new. The oldest, Kaua‘i, was formed only about 5 million years ago. Much of the terrestrial biota may be descended from ancient ancestors that came from older islands now long submerged.

Wilson’s discovery came at a crucial time for evolutionary biology. It has provided an interpretative background particularly for research on the evolution of the terrestrial fauna and flora of the Hawaiian archipelago.

After the basic systematics and geographical distributions had become clear, genetic and behavioral research on the Hawaiian drosophilids was concentrated in two main areas. These have been: 1) the detailed phylogenetic history of a special clade of about one hundred species of the subgenus *Drosophila* (the “picture-winged” flies) and 2) the population genetics and sexual behavior of one exemplary species, *Drosophila silvestris* (Perkins). This paper provides short reviews of the relevant findings and evaluates their impact on evolutionary biology as a whole.

Genetic Tracing of Phylogenetic Histories

Endemic Hawaiian Drosophilidae number about 1,000 species with over 400 species yet to be described (O'Grady *et al*., 2003). The job of cataloguing this immense fauna, begun by Hardy (1965) is still a long way from being completed. Despite great morphological diversity, the endemics are generally referable to only 2 genera, *Drosophil*a and *Scaptomyza* (Kaneshiro, 1976). Any member of this fauna can be easily distinguished morphologically from any of about 20 assorted drosophilid species that have been recently brought into the islands from the continents inadvertently through human activity.

These species are found only on the present high islands, 5 million years of age or less. Although no collections of drosophilid specimens have been made on the older, severely eroded islands, there is strong geological evidence that these islands were once high and presumably forested and thus could have harbored substantial biotas. Indeed, molecular genetic data suggest that the earliest founding event may have occurred about 26 million years ago (Russo *et al*., 1995).

Hawaiian endemics recognized as *Drosophila* fall into 7 groupings for which a preliminary phylogeny has been proposed (see a brief review in O'Grady *et al*., 2003). One of these groups, numbering about 120 species, is the "picture-winged" flies. These occur on all of the high islands from Kaua‘i southeastward, and are the focus of this paper. Studies of band sequences of the giant chromosomes show striking similarities to certain subgenus *Drosophila* species endemic to Hokkaido and the Pacific northwest of the United States (Stalker, 1972; Narayanan, 1973). The data indicate a boreal origin for the picture-winged species from the Bering Archipelago.

Characteristically, males of most of these species show elaborate secondary sexual characters that are both behavioral and structural. As in many other dipteran faunas, male secondary sexual characters have been prominently used for taxonomic purposes. Although morphological differences between the sexes are present in most drosophilids, the extent of elaborate male characters and territorial behavior is especially developed in Hawaiian *Drosophila*, prompting the late Professor Theodosius Dobzhansky to refer to them as the "birds of paradise of the *Drosophila* world".

With proper inducement, a single wild-caught picture-wing female will oviposit in the laboratory, yielding progeny that represent the natural insemination of the wild female. This "isofemale" procedure has made it possible to accurately match males and females of the same species, a process that is often difficult to do when sorting collections from the wild. Isofemale lines thus provide accurate systematic vouchers, especially for genetic studies that can only be done using larvae. In many cases, long-standing laboratory isofemale cultures of each species have been available for laboratory study.

Inversion Markers as Tracers of Relationships Between the Species of Picture-Winged *Drosophila*

Each of the 5 major giant chromosomes of the picture-winged *Drosophila* species displays about 500 chromatic bands in a linear order. Deletion of only a small number of these bands anywhere in these chromosomes is generally lethal, indicating that at the molecular level the bands are the physical sites of important genes. Although the chromosomes of each of the species studied display virtually all of these bands, the linear order of bands varies extensively within each chromosome. Changes in band order are caused by precise measurable chromosomal inversions that occur naturally. An inversion is the result of 2 simultaneous natural breaks in a chromosome, followed by a re-integration of the broken piece, creating a new linear order. The fact that 2 breaks occur simultaneously results in an easily readable chromosomal "marker" that is both unique and permanent, since the probability of a simultaneous occurrence of 2 identical breaks is very small.

Each inversion arises in the germ line of a single individual male or female at one time and place. If it survives and is passed on to progeny, it may be ultimately transmitted to some or all descendent members of the same species. Clearly it must begin as a heterozygote, after which it may come to replace the original order in certain populations. Thus, the probability of survival into future populations is assured if the new variant becomes homozygous, completely replacing the ancestral non-inverted sequence.

Table 1. Ancient theoretical *Drosophila* picture-winged founders from Kaua‘i and their 95 descendents on the newer islands. The total number of species that have been chromosomally sequenced for this study is 107(see Carson, 1992).

ANCESTORS	DESCENDENTS
Six single founders that left Kaua‘i, and a list of Kaua‘i species*, to which each founder was closely related by one or more unique inversions	Lineages of species on the newer islands (number of species on each island)
“*ornata*-related” (1 species only)	*adiastola* group = 15 species (O‘ahu - 2, Maui Nui - 11, Hawai‘i - 2) [For a detailed phylogeny, see Fig. 1]
“*picticornis*-related” (1 species only)	*planitibia* group = 16 species (O‘ahu - 4, Maui Nui - 9, Hawai‘i - 3)
“*sejuncta*-related” (1 species only)	*sejuncta* group = 3 species (O‘ahu - 0, Maui Nui - 1, Hawai‘i - 2)
“*ocellata*-related” (1 species only)	*punalua* group = 5 species (O‘ahu - 3. Maui Nui - 1, Hawai‘i - 1)
“*glabriapex*-related” (2 species)	*glabriapex* group = 24 species (O‘ahu - 12, Maui Nui - 7, Hawai‘i - 5
“*craddockae*-related” (4 species**)	*grimshawi* group = 32 species (O‘ahu -7 , Maui Nui -13, Hawai‘i -12
Total: 6 ancestors	**Total: 95 descendent species** (O‘ahu - 28, Maui Nui - 42, Hawai‘i - 25)

* Kaua‘i has 12 endemic picture-winged species, including *D.attigua* and *D. primaeva*. The latter is judged to be the closest species to a hypothetical ancestor of all the picture-winged species.

** The species shared by Kaua‘i and O‘ahu that morphologically resembles *D. grimshawi* of Maui Nui is now recognized as *D. craddockae* (Kaneshiro & Kambysellis, 1999)

Approximately 200 inversions have been discovered and given individual names in the order of discovery (Carson, 1992). For example, in chromosome 2, the first inversion found was named “2a”, the second “2b” and so on. In some cases, the alphabet, when exhausted, has been used again employing superscripts such as: “$2a^2$”, “$2a^3$”, etc. The formulae are thus based on unique genetic differences arising in nature from an arbitrarily-chosen “standard” gene order. The essentially uniform sequences in all the chromosomes in one species, *Drosophila grimshawi* Oldenberg of Maui, serves this purpose. Some species groups are inversion-rich so that phylogenetic tracing is robust, as in the *adiastola* and *planitibia* groups. However, in the *glabriapex* and *grimshawi* groups a number of morphologically distinct species have identical inversion formulas. This suggests that the basis of the species differences must lie at the genic and not the gross chromosomal level. Many inversions have been found that are polymorphic, i.e., they coexist with the ancestral sequence in local populations.

When the chromosomal similarities are superimposed on the geographical distribution of each species, it is seen that on the oldest island of Kaua‘i the relatively small number of endemic picture-wings fall into 6 inversion formulae. Each of these appears to represent a separate and unique ancestral source for a phylad of newer species present on the newer islands. Thus, each of the 95 species on the newer islands can be traced back by inversions to one of these 6 separate putative ancestors. This is based on the study of the geographical distribution of these chromosomal variants in species still existing on the island of Kaua‘i (Table 1).

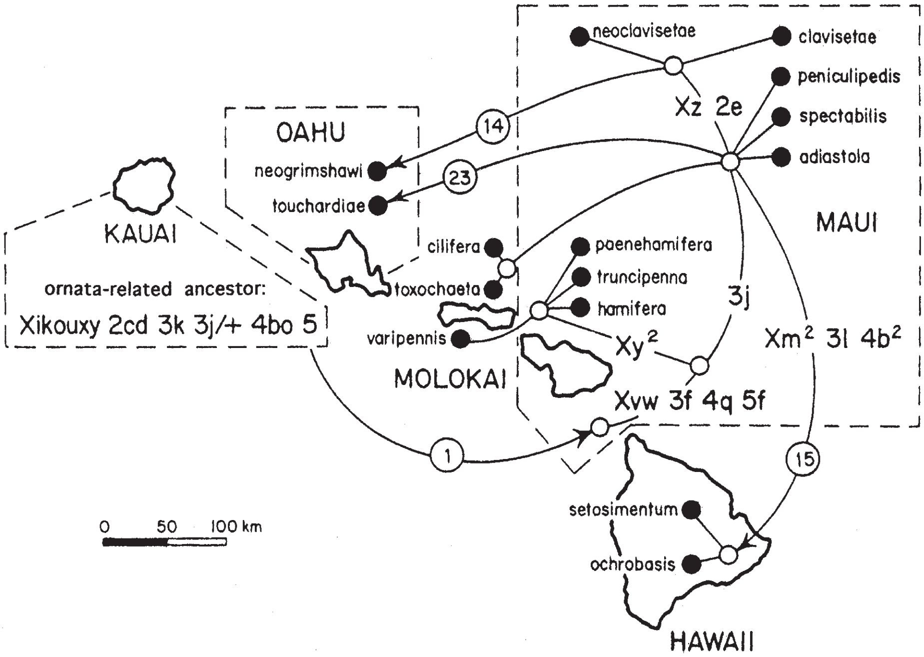

Figure 1. Inversion-sharing phylogeny for 15 species of the *adiastola* group, stemming from an *ornata*-related hypothetical ancestor on Kaua'i. Solid circles: existing species; open circles: hypothetical ancestral populations. Four hypothetical inter-island founder events are indicated (encircled numbers). Procedure: to trace ancestry, start from Kaua'i at the left of the figure where 12 inversions on chromosomes X,2,3,4, and 5 of modern *D. ornata* are listed. These variants were apparently carried by an ancestral founder (#1, encircled) to Maui. After arrival, forms descended from this founder added 5 new inversions in chromosomes X, 3, 4, and 5. After inversion Xy^2 is added, the invariable formula found in each of 4 distinctive modern species (*paenehamifera, truncipenna, hamifera* of Maui and *varipennis* of Moloka'i) is attained. In an alternate pathway, 3j, which has previously been retained in the polymorphic state 3j/+, becomes fixed. This leads to a common ancestor of the 3 species of the *adiastola* subgroup. Only 2 species of the group are found on O'ahu (*neogrimshawi* and *touchardiae*). These show distinctive formulae related to 2 different parts of the Maui phylogeny and are assumed to have arrived in O'ahu separately as "back migrants" from a younger island to an older one (founders 14 and 23). Only 2 species of the group are present on Hawai'i (founder 15). Illustration modified from Carson (1992).

These data are of special interest because of the genetic precision with which the picture-winged species may be grouped and the ancestry of each younger species determined by robust genetic data. A major fact emerging is that there are 95 descendent species that can be identified as endemic to one or more of the 3 newer island groups. This proliferation of species, moreover, is relatively new geologically, since all these species must be younger than the age of the Wai'anae range of O'ahu, i.e., 3.5 million years.

Figure 1 shows a proposed evolutionary scenario for one phylad of species, the *adiastola* group, listed in Table 1. Each species is endemic to the island on which its name appears. Island ages range from about 5 million years for Kaua'i to less than 400,000 years for Hawai'i. This hypothetical phylogeny is useful since the genetic data are superimposed on the geographical distribution of each species. This permits the proposal of intra- and inter-island phylogenies and founder events as explained in the caption. Similar phylogenies for the 5 other groups are given in Carson (1992) or can be located in references to earlier publications.

The phylogenetic differentiation of these species clearly proceeds primarily from older volcanoes to newer ones. One may speculate that the relatively small number of species that have been formed on the 5 volcanoes of Hawai‘i Island is directly related to the geological newness of this island.

New volcanoes appear to be especially open to colonization by waifs from an older volcano and surely the above step-wise pattern is the most prominent one; however, in some cases, the data suggest that richly-speciating groups may include species that have made the colonization from a newer volcano back to an older one. Two cases of this phenomenon involving Maui and O‘ahu are shown in Fig. 1.

Most of the inter-island movements of these drosophilids appear to be best explained by the "founder principle" (Giddings *et al*., 1989). This suggests the inter-volcano and inter-island speciation events are strongly influenced by the constraints of the separation of populations by distance, which, in the case of new lava flows, may sometimes be very small. The above point brings us to a consideration of the data that exist on the dynamics of genetic change within individual populations of these island species.

Evolutionary Processes Within Populations

A large recent body of behavioral data from diverse animal and plant species strongly supports the conclusion that mate or gamete choice, especially by the female, is a significant driving force for genetic change in populations. I have recently pointed out that, if this theory is valid, it will be necessary to reinterpret the basic mode of selection in natural sexual populations. This will include reexamining the relationship between natural and sexual selection in wild populations (Carson, 2002, 2003).

Although little experimental work has been done, review of the data on mating patterns in insects strongly supports choice theory based on female choice of mate (Eberhard, 1996). The complex sexual behavior of the Hawaiian picture-winged species *Drosophila silvestris* has been shown to conform to this idea (Carson, 2002).

About 1970, when the phylogenetic tracing studies of the picture-winged Hawaiian *Drosophila* species had been largely competed, intensive population genetic work began on *Drosophila silvestris*. This species belongs to the *planitibia* group (Table 1) and is one of 3 species of this group that is endemic to the island of Hawai‘i.

Drosophila silvestris is a useful choice for 2 reasons. First, it represents a genetically variable, recently-evolved endemic found on 5 successively younger volcanoes on the newest island, Hawai‘i (Carson, 1982; Craddock & Carson, 1989). Secondly, it manifests a highly complex mating system involving female choice that gives evidence of being in a state of active genetic change in certain populations on Hawai‘i (Carson, 1982, 2002).

Kohala volcano (age about 400,000 years), Hualalai, and Mauna Kea, like all the older volcanoes, appear to have ceased volcanic activity, whereas the 2 most recent volcanoes, Mauna Loa and Kīlauea, are currently active. A comparable range of geological activity is not found elsewhere in the archipelago. Phylogenetically, *D. silvestris* is particularly close to the chromosomally monomorphic species *D. planitibia* Hardy of Maui. These 2 species have a virtually identical basic inversion formula, although *silvestris* has many new added inversions that are polymorphic only within that species. Thus it has been hypothesized that the initial population of *silvestris* on the newer island was established from a founder individual (or individuals) arising from an ancient *planitibia*-like ancestor from Maui. In space and time, therefore, Hawai‘i Island presents a very promising set of populations that may be in an active state of genetic differentiation from older to newer lava flows.

Within each local population, *silvestris* displays a number of specific inversion polymorphisms and electrophoretic variations that differ in frequency from one population to the next. These can be used to make a set of hypotheses relating to the pattern of its intraspecific phylogenetic differentiation from volcano to volcano stressing novel genetic change that has occurred very recently within a single species (Kaneshiro & Kurihara, 1981; Craddock & Carson, 1989).

Sexual Behavior and Mate Choice

Like the ancestral Maui species of this group of picture-wings, sexual behavior at maturity is highly complex. Individuals mature slowly and have substantial longevity in the cool upland environments. Mature males seek out and apparently accumulate on the scapes of single tree ferns (*Cibotium* spp.) in groupings of 5–10 individuals. Each male patrols his own individual lek, aggressively defending it from all intruders. Females visit these leks, stimulating the initiation of courtship by the male. Despite this, copulation is very rarely observed in natural leks. The implication of these rarely-observed matings is that females move between leks but only very rarely is a male accepted.

In the laboratory, courtship between pairs of flies placed in chambers is often long and complicated, with the female frequently decamping to the degree possible in the artificial chamber. This may extend over many hours and "pair-matings" frequently fail to be consummated. The male approach to the female begins with persistent frontal displays and circling by the male from some distance away. In group experiments, many individual males are rejected.

While imperfectly mimicking the natural leks, quantitative studies of mating behavior in small plastic cages have yielded valuable information on copulation patterns. Tree fern leks are simulated by placing 10 to 12 mature, healthy, individually marked, virgin males into a clear plastic cage with perches and available food. After a period of several days for male environmental adjustment, a single mature virgin female is introduced for a one-half hour period. If there is no copulation during this time, the female is removed and replaced by another one. A copulating pair is covered with a glass vial until separation, after which the female is removed and her offspring reared. Each male is returned to the cage following separation. Each experiment is repeated with the same males over 6 days

A striking result is obtained (Carson, 2002). One-third of the males in the cages are rejected by all introduced females and remain un-mated over the week of testing. These may be designated as the "duds". In contrast, a separate one-third of the males are repeatedly accepted by a newly introduced female, often on a daily basis ("studs"). The final one-third consists of males accepted only a few times during the week of tests. All males are mature, healthy and court actively under these conditions.

The restrictive complications of sexual selection in *silvestris* appear not to be confined to that species. Although the behaviors of individuals in only a few other species of Hawaiian *Drosophila* have been studied quantitatively, the general importance of female choice can be inferred. Indeed, female choice may be characteristic of other drosophilids and possibly many other animals and plants.

Some Theoretical Questions and Conclusions

Why do these insular populations of Hawaiian *Drosophila* show such a continuous formation of new species? Why are the mating systems so profoundly exaggerated by constantly changing sexual selection as these new species are formed in this serial fashion? Why should behavioral sexual selection have so much strength as these species evolve allopatrically on what are basically new substrates provided by emerging linear, spatially separated shield volcanoes? What is the relationship between natural and sexual selection? I suggest that the findings in Hawaiian *Drosophila* may provide the basis for a few tentative working hypotheses.

Natural Selection Subsumes Sexual Selection

The Darwinian view that natural selection is ubiquitous is adopted here as the guiding principle in all populations. Eliminative natural selection takes a continually heavy toll, so that relatively few individuals of a natural population survive to the reproductive phase. As sexual maturity is reached in the populations of a species, the general pressure on the selection system shifts from survival to mechanisms that place those individuals that have survived to adulthood through a series of tests that force differential reproduction among them.

In the above process, choice of mate appears to be an all-pervasive, but often cryptic guide to this process (Carson, 2003). In my view, sexual selection emerges, not a separate process, but one that functions as a greatly refined extension of natural selection that serves to optimize the passage of adaptively superior DNA to the ensuing generation. This is the essence of Darwinian fitness.

Nature provides the female with a choice system that will enable the diagnosis of fitness of the male through various devices, such as male-to-male combat, lek displays, resistance to parasites and other environmental hazards.

This is where the subject of genetic variability among males must be addressed. Recombining sexual gene pools are far more complex than has been realized. The presence of genome-wide systems of balanced polygenic polymorphism undergoing recombination, especially in the female, is able to create fields made up of unique genetically variable males. This genetic variability confronts the choice mechanism of females.

Choosing females appear to be assessing male fitness by using many clues. Most particularly, they may be able to use discriminatory devices to sort out genetically based fitness qualities of their prospective mates. Much is yet to be learned about how this is accomplished and I see this as a major future challenge to genetically based ethology.

Active genetic change and species formation comparable to that of *Drosophila* is also observed among the majority of the endemic Hawaiian terrestrial biota of other insects, birds, snails and flowering plants (Zimmerman, 1948; Hubbell, 1968; Kay, 1994; Wagner & Funk, 1995).

Is the evolutionary process that has allowed formation of these new forms uniform throughout the geography of the islands or is there a special geographical or geological area where evolutionary change is concentrated? I suggest the facts support the latter view. Active eruptive zones and formation of new sterile surface lava is now, and has been for at least 20 million years, confined to a very small zone of the archipelago that lies above the Hawaiian hotspot. As the Pacific plate moves northwestward, it carries the aging lava flows and their volcanoes away from the extremely narrow region where active volcanism is at work.

At the time of formation, the lava is sterile and forbidding to most life but will immediately see the arrival of propagules from adjacent older flows. As the plate moves, volcanism will slowly cease and the flow of successful colonists will facilitate the emergence of a new ecosystem. Such colonists will face maximal environmental challenges to both the survival and reproductive phases of natural selection. Thus the volcanic hotspot continually spawns a long-persisting "evolutionary hot-spot" in the area directly above it.

Such a diagrammatic situation is rarely if ever found elsewhere in the world although short-term volcanic challenges characterize many single isolated oceanic islands as well as oceanic archipelagos with irregular volcanism such as Galápagos, the Societies, and the Canary Islands (Carlquist, 1965). In most of these cases, however, the volcanic challenge may be of relatively short duration rather than continuous as in Hawai‘i, but volcanism may challenge genetic systems to yield isolated bursts of species. These are likely to be briefer episodes than those occurring in the long-lasting Hawaiian case where some lineages have been through the process earlier.

Most continental biota have come to some degree of ecological stability, characterized by broad patterns of gradual geographic change. Nevertheless, exuberant sexually reproducing, cross-fertilizing systems can be intensified in some special geographic sites. For example, such areas are found on the high, immobile continental volcanoes of Africa (Hedberg, 1970).

A case of genetic systems even closer to what is found in Hawai‘i occurs in association with the geological revolutions associated with the actively spreading east rift zone of Africa. The cichlid fish fauna in the geologically new African lakes is one of the evolutionary wonders of the world (Echelle & Kornfield, 1984; Goldschmidt, 1996). Hundreds of species in single lakes are not only strongly adapted locally but, like in Hawaiian *Drosophila* they have developed what appear to be novel sexual selection systems that parallel those found in Hawaiian drosophilids. Thus, the development of the reproductive systems in cichlids appears to be a process that reinforces mate choice and Darwinian fitness as an intra-population outcome of natural selection. In both faunas, natural selection drives genetic change that is based on selection for intra-population fitness rather than selection for inter-specific isolation.

Acknowledgments

I dedicate this paper to the memory of valued colleagues now deceased: Frances E. Clayton, Theodosius Dobzhansky, Wayne C. Gagné, Joseph Grossfield, D. Elmo Hardy, Walter E. Johnson, Herman T. Spieth, Harrison D. Stalker, Wilson S. Stone, and Haruo Takada.

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Phylogenetic Relationships Within the *Drosophila haleakalae* Species Group Inferred by Molecular and Morphological Characters (Diptera: Drosophilidae)

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Abstract

The *Drosophila haleakalae* species group, the most basal lineage within the Hawaiian *Drosophila* lineage, consists of 54 described species placed in 5 subgroups. Previous taxonomic studies, initiated by Elmo Hardy, have provided an excellent groundwork on which to base further evolutionary studies. We present a phylogenetic hypothesis of the *Drosophila haleakalae* species group using a suite of morphological, behavioral, and molecular characters (including 5 newly developed nuclear gene regions) that is more resolved and better supported than any previous phylogeny of this group. We use our phylogeny to refine and revise the taxonomic relationships of species in the *haleakalae* species group.

Background

Soon after Elmo Hardy arrived at the University of Hawai‘i in 1948, he began collaborating with E. C. Zimmerman to treat the endemic Hawaiian Diptera, an ambitious task that eventually resulted in 5 volumes in the Insects of Hawai‘i series and an impressive series of additional publications (Evenhuis & Thompson, 2003). After starting work at UH Mānoa, Elmo began to accumulate data on the known Hawaiian Diptera (Hardy, 1952), as well as make collections of hundreds of new drosophilid species. The years 1950–1959 were filled with inter-island travel, often via boat or prop plane. For example, during April–August 1952, Elmo made collections on O‘ahu, Maui, Moloka‘i, Lāna‘i, Hawai‘i, and Kaua‘i. He repeated this during the same period in 1953 and made similar expeditions in 1956, 1958 and 1959 (Hardy *et al.*, 2001). The largest and most diverse group that Elmo began to study in those early years was the Hawaiian Drosophilidae.

The early 1960s were an exciting time to study Hawaiian Drosophilidae. Not only did Elmo continue to collect and describe new species, he initiated the Hawaiian *Drosophila* Project with collaborators at the University of Texas and other institutions (Spieth, 1980, 1981). This joint NSF-NIH initiative began in 1963 with the goal to understand all aspects of the basic biology of the endemic Hawaiian Drosophilidae. Elmo's contributions to this project, along with the studies of Hamp Carson, Bill Heed, Herman Spieth, Ken Kaneshiro and others, have made the Hawaiian Drosophilidae one of the most powerful evolutionary model systems and the best documented example of adaptive radiation in nature (Craddock, 2000). Critical to the success of this work was the publication of Elmo's revision of the Hawaiian Drosophilidae, a work that included a treatment of all 400 drosophilids known from Hawai‘i at that time, about 350 of which were newly described (Hardy, 1965). Subsequent publications extending into the late 1970s, many in collaboration with Ken Kaneshiro, added over 100 more species to this fauna.

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When Elmo retired from the University of Hawai'i in 1980, one major revision remained to completed, a treatment of the so-called "fungus feeder" species group. When Herman Spieth developed the now standard "mushroom tea" bait in the late 1970s, a whole new fauna of mycophagous *Drosophila* were discovered. Elmo, along with Kenneth Kaneshiro, began a revision of this new material during the 1970s. However, because of retirement and other concerns, their study was never published. Through the 1980s and 1990s various students and post-docs worked on the manuscript, but the general content of the work remained as Elmo and Ken had left it in 1980. Chica do Val and one of us (O'Grady) began to revise this work during the summer of 1999 and published it (Hardy *et al.*, 2001), renaming the group *haleakalae*, after a name first used by Elmo Hardy (1965).

Our work on the *haleakalae* revision has in turn stimulated additional research. For example, I was very interested in understanding the phylogenetic relationships among species in this enigmatic group and thought that DNA sequences might be able to resolve some issues that morphology alone could not. Martine Zilversmit and I present the results of this research here. It is a pleasure to dedicate this paper to the memory Dr. Elmo Hardy, a man whose long career and diligent work has had a significant impact not only on the Hawaiian Drosophilidae, but many other groups of Diptera (*e.g.,* Tephritidae, Bibionidae, Pipunculidae, Dolichopodidae) as well.

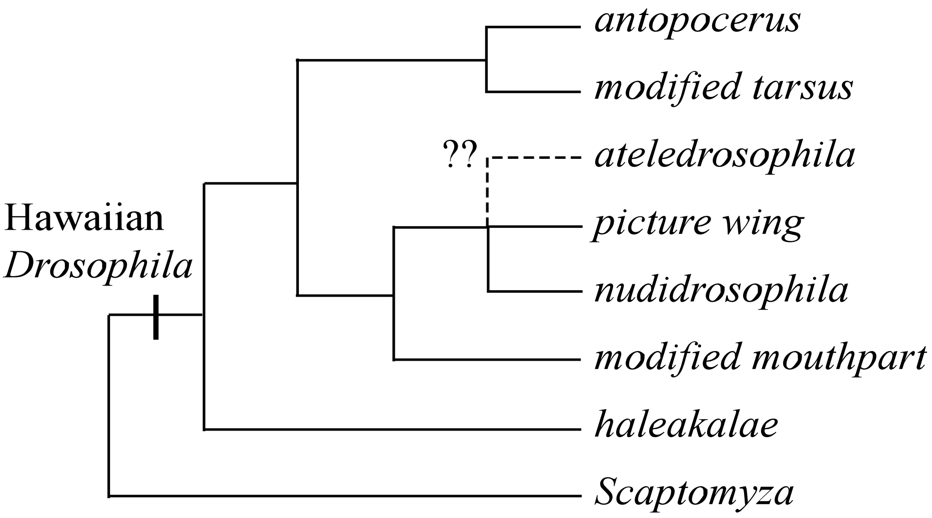
Introduction

The Hawaiian Drosophilidae consists of two major lineages, Hawaiian *Drosophila* and the genus *Scaptomyza* (Fig. 1; Bonacum, 2001; O'Grady, 2002; O'Grady *et al.*, 2003; Remsen and O'Grady, 2002). Within the Hawaiian *Drosophila* lineage, there are currently 7 recognized species groups (*antopocerus*, *ateledrosophila*, *haleakalae*, modified mouthpart, modified tarsus, *nudidrosophila*, picture wing). The *haleakalae* species group is the most basal and contains a total of 54 species, all of which are endemic to the Hawaiian Islands (Hardy *et al*., 2001). Although this group was first formally proposed and named by Hardy *et al*. (2001) it has been known by a variety of names over the past 40 years, including "fungus feeders", "rimmed labellum", and "white (or light) tipped scutellum group" (e.g., Heed, 1968; Spieth, 1966; Throckmorton, 1966). Based on morphological characters, Hardy *et al.* (2001) divided this group into 6 subgroups: *anthrax*, *cilifemorata*, *haleakalae*, *luteola*, *polita*, and *scitula*. These characters, however, consisted of only a few "key characteristics" that were used to separate species and were never analyzed using cladistic methods. The potential suite of morphological characters available to examine relationships in this group was not yet comprehensively surveyed.

Throckmorton (1966) listed a number of synapomorphies for the *haleakalae* group, including male genitalia lacking anal sclerite, short filaments on eggs, and females with weakly sclerotized, non-telescoping and non-functional spermathecae. Spieth (1966) also observed that all members of this group lack the elaborate courtship displays seen in the other major lineages of Hawaiian *Drosophila*. Several molecular studies have tested the monophyly of this group in a maximum parsimony framework (Kambysellis *et al.*, 1995; Baker & DeSalle, 1997; Bonacum, 2001), but none sampled extensively within the *haleakalae* species group.

Bonacum (2001), who used about 3.3 kb from four loci (16S, COI/COII, *Adh, Gpdh*) to examine phylogenetic relationships among the major Hawaiian drosophilid lineages sampled more extensively within the *haleakalae* group than any other previous study. He included 13 *haleakalae* group species in his study (Fig. 2). Only 3 nodes showed significant bootstrap support: (A) *D. nigella-D. fungiperda*, (B) *D. nigella-D. fungiperda-D. nigra* and (C) *D. inciliata-D. longiperda*. Nodes A (*fungiperda* complex) and C (*venusta* cluster) correspond well with the taxonomy proposed by Hardy *et al*. (2001). Node B suggests that the *cilifemorata* cluster may not be monophyletic due to the placement of *D. nigra* as the sister of the *fungiperda* complex. This grouping makes sense from a morphological standpoint, however, because all 3 taxa lack a rimmed labellum.

We analyzed a total of 18 ingroup and 3 outgroup taxa in order to test the monophyly of the *haleakalae* species group and its component subgroups using a combination of characters. A total of 87 morphological and behavioral characters were scored and analyzed using maximum parsimo-



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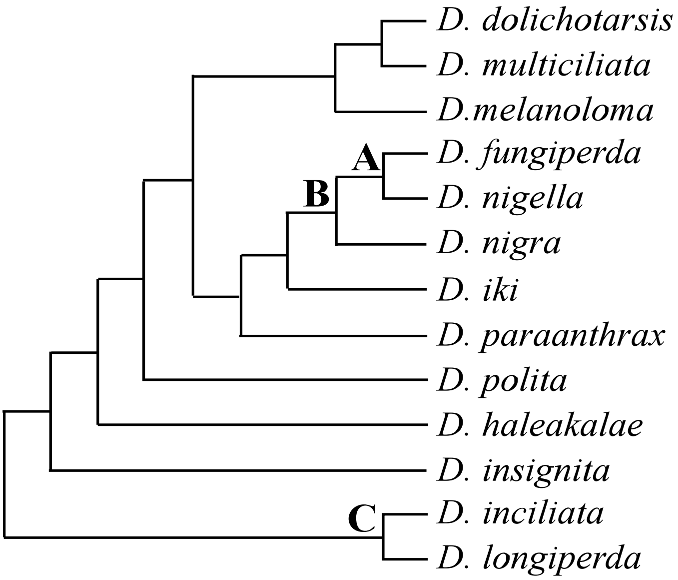

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Figure 1. Phylogenetic relationships among the major lineages of the Hawaiian Drosophilidae. **Figure 2.** Phylogenetic relationships within the *haleakalae* species group, after Bonacum (2001). Letters at the nodes indicate those relationships which were strongly supported by bootstrap proportions.

ny. The molecular matrix, containing over 5000 characters from eight rapidly evolving gene regions (COII, *sia, glass, l(2)not-1*, *Marf*, *Rpt4*, ITS-1, *snf*) and a presence-absence insertion-deletion (indel) matrix was also analyzed using maximum parsimony. Maximum likelihood was employed to further analyze the molecular loci, both individually and in combination with one another. Finally, a data set consisting of both molecular, morphological, behavioral, and indel characters was analyzed using maximum parsimony.

Our results suggest strong support for the monophyly of the *haleakalae* species group. While a number of previously proposed (Hardy *et al.*, 2001) clades are supported in the current study, several novel relationships are also observed. While the individual molecular and morphological analyses are largely unresolved, much stronger support is seen in the combined analyses. The approach taken in the current study highlights the benefit of using all available sources of character information including molecular, morphological, and ecological when inferring phylogenetic relationships.

Materials and Methods

Taxon Sampling

Taxa and localities sampled are listed in Table 1. Ingroup taxa were selected in order to sample from each major lineage within the *haleakalae* species group. Outgroup taxa were selected from 3 other Hawaiian *Drosophila* species groups: the picture wing (*D. crucigera*), modified mouthpart (*D. mimica*), and modified tarsus (*D. petalopeza* for the COII partition, *D. waddingtoni* for the *glass* partition, and *D. quasiexpansa* for all other data partitions).

Morphological and Behavioral Characters

A total of 87 morphological and behavioral characters were scored. The morphological characters were from external adult structures (this study), as well as internal morphology and immature forms (after Throckmorton, 1966). External adult structures were scored after surveying the literature (Hardy, 1965; Hardy *et al.*, 2001) and examining at least 10 individuals. Behavioral characters were scored after Spieth (1966).

Template Selection

With the exception of COII and ITS, the 8 loci we used were selected based on a previous study designed to examine phylogenetic relationships within the family Drosophilidae (Zilversmit *et al.*, 2002b). All sequences in the present study were chosen based on (1) the ease of amplification and sequencing and (2) because they appeared to be accumulating variation at a rate that would provide resolution at the species-level (based on the number of parsimony informative characters for each partition found in the pilot study).

Additional characters, generated by scoring indel events in the non-coding region of the *Marf* locus, were also analyzed. This region yielded a total of 68 characters, 24 of which were parsimony informative. All indel characters were considered discrete and were scored as either present or absent. The majority of indels were small (4–6 base pairs) and were present (or absent) in only a few taxa. Overlapping gapped regions were considered individual, discrete characters, rather than continuous varieties of the same character (Simmons & Ochoterena, 2000; Simmons *et al.*, 2001).

DNA Isolation and PCR Amplification

In most cases, DNA was prepared from multiple flies (3–5). *Drosophila dolichotarsis* DNA was generated using a single fly. Flies were macerated using a micro pestle in a 1.5 ml PCR tube with buffer provided by the DNeasy Tissue Kit and DNA was isolated using the standard protocol supplied in the manufacturer's instructions (Qiagen). Loci of interest (above) were PCR-amplified using primers described in O'Grady (1999) and Bonacum (2001) employing the protocols of Zilversmit *et al.* (2002a). All sequences have been submitted to GenBank under accession numbers AY343526-AY343539 and AY348178-AY3481290. Several taxa are missing sequences for *glass*, *snf* and *Rpt4* as they were unable to be amplified from these templates.

Table 1. Taxonomy and Collection Information of Species Sampled

Group	Subgroup	Species	Collection Locality[1]
haleakalae	*anthrax*	*melanoloma*	MOLOKA'I: Pu'u Kolekole, 19—21.iii.1999, OG58.6, PMO&JBS
		multiciliata	HAWAI'I: Kipuka #9, Saddle Road, 5100 ft., 12.i.1988, Y37, RD
	cilifemorata	*longiperda*	HAWAI'I: Ola'a Forest, Volcanoes National Park, 14—15.iii.1989, Y57, RD,JS&KS
		dolichotarsis	MAUI: Waikamoi Forest Preserve, 7—8.vi.1997, Z35, MPK,CM&SLM
		iki	MAUI: Waikamoi Forest Preserve, JB&MPK
		nigra	MAUI: Waikamoi Forest Preserve, JB&MPK
		insignita	O'AHU: Makua Valley, 20.ii.2000, OG86.1, PMO,JBS&SLM
	haleakalae	*ochropleura*	HAWAI'I: Greenwell Ranch, Pauahi, Kona, 18.ii.2000, OG84.1, PMO&JBS
		fungiperda	HAWAI'I: Kaloko Mauka, North Kona, 3.vii.1998, OG38.5, PMO&SLM
		nigella	MAUI: Waikamoi Forest Preserve, JB&MPK
		haleakalae	MAUI: Paliku Cabin, Haleakala, 6400 ft., 3.viii.1988, Y50, KYK,RD,RA&WDP
	polita	*bipolita*	O'AHU: Ekahanui Gulch, Waianae Mountains, 10.ii.2000, OG75.5, PMO,MPK&SLM
		canipolita	O'AHU: Makua Valley, 20.ii.2000, OG86.2, PMO,JBS&SLM
		paraanthrax	KAUA'I: Pihea Trail, Na Pali Kona Forest Preserve, 25.ii.2000, OG89.2, PMO&JBS
		polita	HAWAI'I: Greenwell Ranch, 12—14.iii.1989, Y56, KYK,RD,JSY,KSY&RDS
	scitula	*fulgida*	KAUA'I: Honapu Ditch Trail, Puu Ka Pele Forest Preserve, 24.ii.2000, OG87.9, PMO&JBS
		melanosoma	KAUA'I: Honapu Ditch Trail, Puu Ka Pele Forest Preserve, 24.ii.2000, OG87.8, PMO&JBS
		scitula	KAUA'I: Honapu Ditch Trail, Puu Ka Pele Forest Preserve, 24.ii.2000, OG87.E, PMO&JBS
mod. mouthpart		*mimica*	HAWAI'I: Hawai'i Volcanoes National Park, JB&MPK
modified tarsus		*petalopeza*	MAUI: Upper Waikamoi Forest Preserve, 6.vii.1998, OG41.2, PMO&SLM
		waddingtoni	MAUI: Heed Trail, Waikamoi Forest Preserve, 2.vi.1999, OG71.A, PMO
		quasiexpansa	MAUI: Upper Waikamoi Forest Preserve, 6.vii.1998, OG41.E, PMO&SLM
picture wing		*crucigera*	O'AHU: RD&KYK Collection, W41N3

[1] Collector Abbreviations: CM = Cam Muir; JB = James Bonacum; JBS = Julian B. Stark; JSY = Jong Yoon; KSY = Kay Yoon; KYK = Kenneth Y. Kaneshiro; MPK = Michael P. Kambysellis; PMO = P. M. O'Grady; RA = Ross Antonson; RD = Rob DeSalle; SLM = Steven L. Montgomery; WDP = William D. Perreira

Table 2. Summary of Maximum Parsimony Analyses.

Partition	# Characters	#PICs[1]	%PICs	#MPTs[2]	# Steps	CI[3]	RI[4]
All Data	5121	508	—	2	2295	0.723	0.501
molecular	4966	431	85	3	1999	0.75	0.513
nuclear	4278	322	63	5	1520	0.824	0.599
COII (mt)	688	109	21	3	459	0.538	0.408
sia	462	14	3	50,000+[6]	106	0.925	0.75
glass[5]	613	23	5	24	95	0.937	0.842
ITS-1	661	81	16	612	327	0.838	0.685
l(2)not-1	638	83	16	878	228	0.811	0.684
snf[5]	467	26	5	6	178	0.933	0.714
Marf	954	113	22	16	467	0.857	0.73
Rpt4[7]	483	21	4	nd	nd	nd	nd
indels	68	24	5	27	71	0.915	0.846
morphology	87	53	10	36	193	0.487	0.533

1. Parsimony Informative Characters.
2. Most Parsimonious Trees.
3. Consistency Index.
4. Retention Index.
5. Sequences available from only a subset of taxa. Searches with cg3455 not attempted, only four taxa determined.
6. Search could not be completed due to lack of memory (too many equally parsimonious trees). Maxtrees set to 50,000 for *sia* search.
7. Search not done because only a few taxa amplified for this locus.

Sequence Editing and Phylogenetic Analysis

All sequences were edited in Sequencher 4.0 (Gene Codes Corp.) and exported into NEXUS formatted files (Maddison *et al.*, 1999). Alignment for protein coding sequences was trivial and was done manually. Non-coding regions were also aligned manually using MacClade (Maddison & Maddison, 2000). Alignments are available from the authors by request.

Phylogenetic analyses, using both maximum parsimony (MP) and maximum likelihood (ML) algorithms, were done in PAUP* 4.0b10 (Swofford, 2003). In addition to analyzing all data in a simultaneous analysis (Nixon & Carpenter, 1996), we also partitioned the data as follows: morphology and behavior alone, all molecular characters, nuclear loci, mitochondrial loci, and individual analysis of all partitions (COII, ITS, *Marf*, *sia, snf, glass, l(2)not*, indels). Settings for MP analyses were as follows: search type = heuristic, addition sequences = random, number of replicates = 200, branch swapping = TBR. Support at each node was assessed using bootstrap proportions (BP; Felsenstein, 1985, 1988) and Jackknife (JK; Farris *et al.*, 1996) with 200 bootstrap or jackknife replicates (other settings as above). Uninformative characters were excluded for bootstrap replicates. Jackknife was done using a 37% deletion with the emulate Jac resampling option selected. Decay indices (Bremer, 1988) and partitioned branch support (PBS; Baker & DeSalle, 1997) were calculated using TreeRot (Sorenson, 1999).

Modeltest (Version 3.06; Posada & Crandall, 1998) was used to determine optimal models and model parameters for both individual and combined molecular partitions. These models were then used in ML searches with the following settings for individual loci: search type = heuristic, addition sequences = random, number of replicates = 10, branch swapping = TBR. Combined analyses (all data, nuclear loci, etc) were done with the above settings but using 100 replicates. Support was assessed using 100 bootstrap replicates (settings as above).

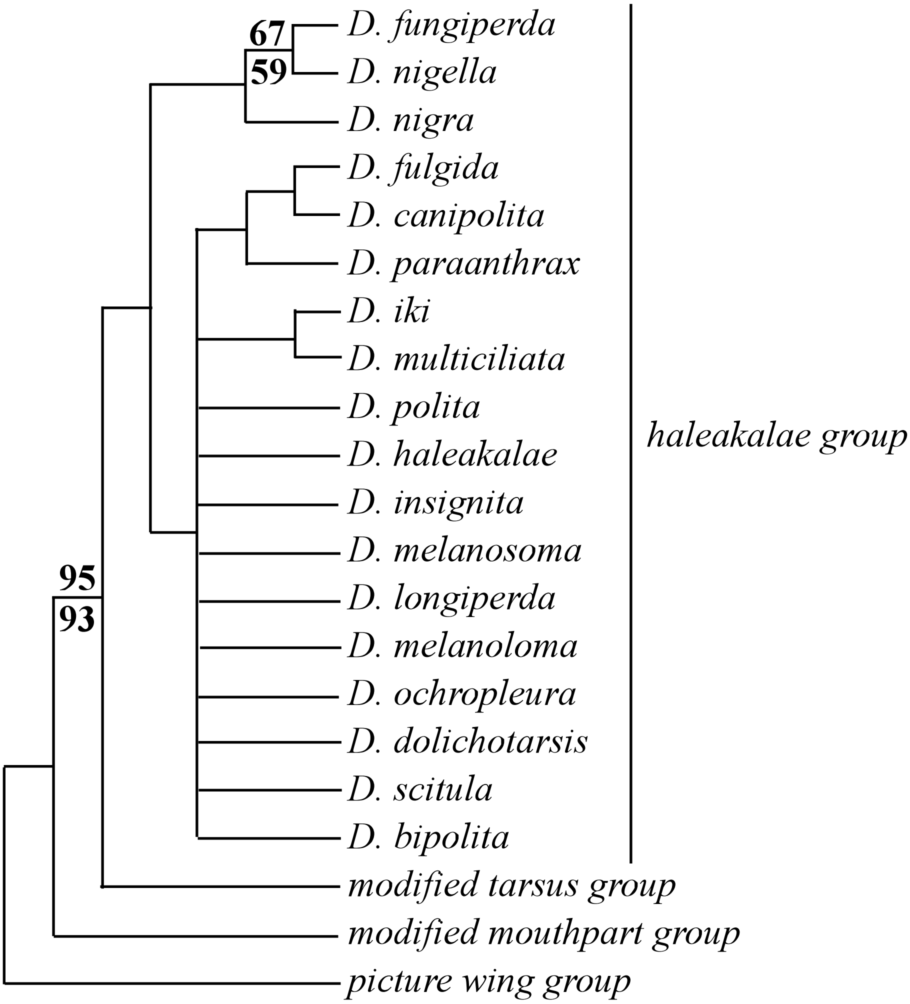

Figure 3. Morphological hypothesis of relationships within the *haleakalae* species group. Phylogeny shown is a strict consensus of 36 most parsimonious trees of 193 steps (refer to Table 1 for more information). Bootstrap proportions are above the nodes and jackknife values are below.

Divergence Time Estimation

We used a likelihood ratio test to determine whether the combined molecular data fit the hypothesis of a global clock when tested against the assumption of no clock. The null model was rejected at the P = 0.01 level (Modeltest 3.06; Posada & Crandall, 1998) so we will use a version of the local clock (Yoder & Yang, 2001). Pairwise relative rate tests (outgroup = picture wing group, model = GTR) were performed using HYPHY, version 0.95beta (Kosakovsky-Pond & Muse, 2000) to determine rate classes for various branches. Pairwise comparisons which failed relative rate tests were used in conjunction with ML tree topology to assign various rate classes to nodes in an effort to correct for rate heterogeneity and fit to a local molecular clock (Yoder & Yang, 2000). Divergence times were estimated in PAML, version 3.13 (Yang, 1997) using three calibration points (node 5) *D. nigella-D.*

fungiperda, (node 1) *D. ochropleura-D. haleakalae*, and (node 10) *D. bipolita-D. canipolita-D. insignita*. Nodes 1 and 5 were set to 0.5 and 1.9 million years (MY), the geological age of the Big Island and Maui, respectively. This gives an upper and a lower bound of divergence estimates. Node 10 was set to 3.7 MY, the age of O‘ahu, the oldest island with all three species present. Two different local clocks were used: TREE 1, where one rate class was assigned to *D. fungiperda*, another to *D. fulgida* and a third to all other branches and TREE 2 where one rate class was given to the outgroup, another to the short internodes (Fig. 5), and a third to all other branches.

The calibration point at node 5 is problematic as *D. fungiperda* is involved in many significantly heterogeneous pairwise relative rate tests (data not shown). In fact, *D. fungiperda* and the closely related *D. fulgida* together account for over 2/3 of the significant pairwise relative rate test results. An attempt to correct for this heterogeneity (tree 1, above) still yielded divergence time estimates that were very recent, given the distribution of taxa. For this reason, only points 2 and 3 were used. Values from each estimate were averaged (after Jordan *et al.*, 2003) and are presented in Fig. 6.

Results

Morphology and Behavior

Maximum parsimony analysis of the morphology and behavior data matrix recovered 36 equally parsimonious trees of 193 steps (Table 2). The strict consensus of these trees is largely unresolved (Fig. 3), although there is support for a *nigella-fungiperda* clade (BP = 67, JK = 59) and the monophyly of the *haleakalae* group as a whole (BP = 95; JK = 93). Several other relationships are seen in the strict consensus (Fig. 3), but are not supported in either the bootstrap or jackknife analyses. It is clear that, while over 50% of the characters in this partition are parsimony informative, these aren’t sufficient to provide support for any but the most robust nodes. Sampling additional morphological characters might be possible but, because members of the *haleakalae* group are quite homogeneous with respect to external morphology, this will require extensive scanning electron microscopy and dissection of internal structures.

Individual Analyses of Molecular Partitions

Individual partitions analyzed using MP (Table 2) and ML (Table 3) displayed varying levels of resolution based on a variety of factors (number of parsimony informative characters, signal to noise ratio, inferred base composition and rate matrices, etc.). Not surprisingly, these smaller partitioned data sets were not as well resolved or supported as the larger combined partitions. However, several relationships were common to both the combined and multiple individual partitions and likely reflect cases of strong support in the data. Rather than present each individual phylogeny, we summarize recurring clades, (Table 4; Figs. 4, 5). Of the 14 nodes present in the combined MP search, 10 were recovered in at least 2 individual analyses and over half (6) were supported in 3 or more of the individual searches (Table 4).

Several of these nodes correspond well with the taxonomic groups proposed by Hardy *et al.* (2001). For example, the monophyly of the *haleakalae* group (Fig. 4; node 17) is supported in all of the individual MP analyses, regardless of the partition examined. The *fungiperda* complex (Fig. 4; node 5), is supported in five individual analyses. Interestingly, one other relationship (Fig. 4; node 11) was also found in 5 individual partitions, but did not exactly correspond with any taxonomic group proposed by Hardy *et al.* (Table 5). In this case, a modified version of the *polita* subgroup, including *D. insignita*, should be erected to reflect the recent phylogenetic results (see below).

Individual MP topologies were highly congruent with both individual and combined ML trees (Table 4). Although it is not possible to partition support on the ML trees, the presence of several key nodes (i.e., *haleakalae* group, *fungiperda* complex) in multiple individual ML searches lends support to these relationships (Table 4). Interestingly, those clades present in individual ML analyses, but not seen in corresponding MP trees, were typically supported by a positive partitioned branch support value in combined analyses (Table 4).

Table 3. Summary of Maximum Likelihood Analyses.

Partition	Model[1]	-ln L	G[2]	I[3]	Base Frequencies	Rate Matrix
molecular	GTR+I+G	17878.1191	0.7654	0.3513	A = 0.2776 C = 0.2278 G = 0.2115 T = 0.2831	A-C = 1.0391 A-G = 2.2446 A-T = 1.5406 C-G = 0.9470 C-T = 3.0925 G-T = 1.0000
completed	GTR+I+G	13795.97434	0.7819	0.3521	A = 0.2857 C = 0.2088 G = 0.1962 T = 0.3093	A-C = 1.1412 A-G = 2.2862 A-T = 1.4604 C-G = 1.1112 C-T = 3.3180 G-T = 1.0000
nuclear	HKY+G	14570.5479	0.4135	0	A = 0.2778 C = 0.2303 G = 0.2147 T = 0.2773	TRatio = 0.8687
COII (mt)	GTR+I+G	3344.0908	0.4413	0.4510	A = 0.3278 C = 0.1491 G = 0.1170 T = 0.4061	A-C = 1.0000 A-G = 6.3467 A-T = 1.0000 C-G = 1.0000 C-T = 11.5958 G-T = 1.0000
glass	HKY+G	1474.9418	0.4413	0	A = 0.2417 C = 0.3086 G = 0.2289 T = 0.2208	TRatio = 1.3424
ITS-1	HKY+G	2698.9194	0.7189	0	A = 0.3907 C = 0.1292 G = 0.1237 T = 0.3563	TRatio = 0.5673
l(2)not-1	K80+G	2218.4741	0.3157	0	equal	TRatio = 1.7308
snf	HKY+G	1445.3038	0.6670	0	A = 0.3324 C = 0.2049 G = 0.2332 T = 0.2295	TRatio = 1.0547
Marf	F81+G	3853.4568	0.703	0	A = 0.2671 C = 0.2209 G = 0.2103 T = 0.3017	na

[1] Models of evolution used include: the Felsenstein 1981 model (F81) which allows for unequal base frequencies, the Kimura 2-Parameter model (K80) where base frequencies are equal but transitions and transversions (TRatio) can have different rates, the HKY model which relaxes the equal base frequency constraint of the K80 model, and the General Time Reversible model (GTR) that allows for six rate parameters and unequal base frequencies. Additional parameters inferred were the gamma shape parameter (G[2]) or the percent of invariant sites (I[3]) present.

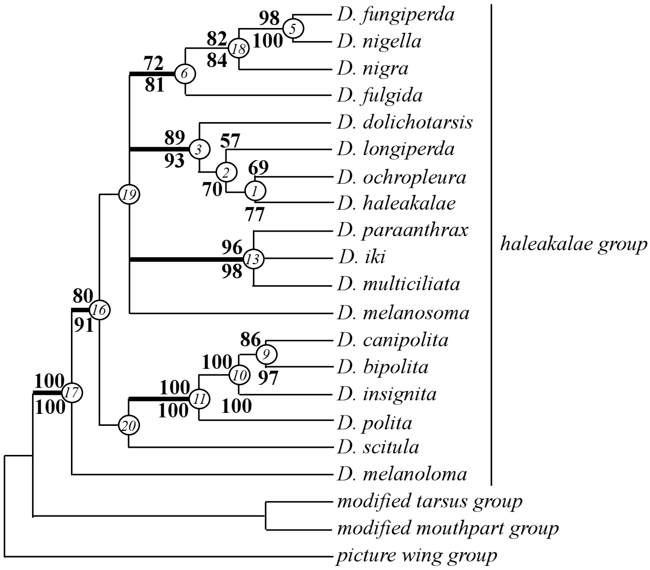

Figure 4. Phylogenetic relationships within the *haleakalae* species group based on maximum parsimony analysis of all molecular and morphological data. Bootstrap proportions are shown above each node, jackknife values are below. Small italic numbers at each internode refer to various clades (see Results; Table 4).

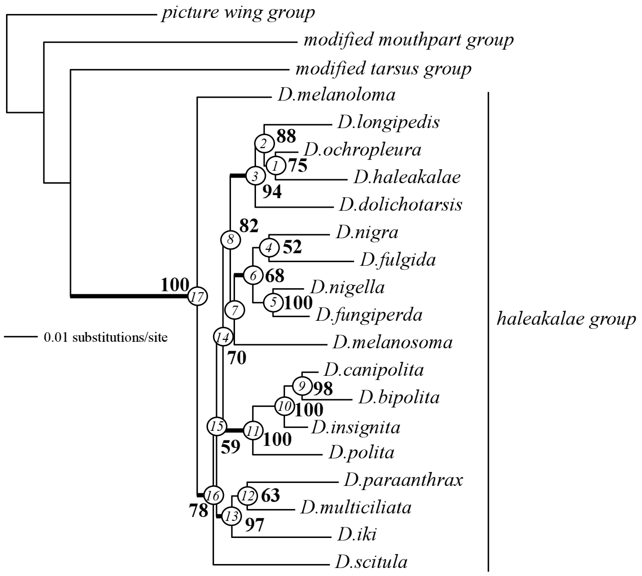

Figure 5. Phylogenetic relationships within the *haleakalae* species group based on maximum likelihood analysis of all molecular loci. Bootstrap proportions are shown above each node. Small, circled italic numbers at each internode refer to various clades (see Results; Table 4).

Combined Analyses

Tree topologies from combined MP and ML analyses are very similar to one another (Figs. 4, 5). Of the fourteen nodes present on the combined MP analysis, 11 were also observed in the combined ML phylogeny. There are only 3 cases where a relationship is supported with MP but not with ML, and only 6 cases where the converse is true (Table 4). These latter differences are due mainly to the differences in support and resolution between the MP tree and the fully resolved ML phylogeny. If one were to exclude those nodes lacking greater than 63% BP in either combined analysis (Figs. 4, 5; nodes 4, 7, 8, 12, 15, 19, 20), only 2 nodes actually differ. Of these, one (Fig. 4; node 18) is observed in partitions for which ML analyses were not tractable (Fig. 3; morphology). The remaining relationship (Fig. 5; node 14) is observed in some individual analyses, suggesting only minimal support (BP = 70%) for these clades in the combined ML analyses. We discuss the ramifications of the current analyses to the taxonomic and phylogenetic relationships of the *haleakalae* species group below.

Phylogenetic Relationships

The *haleakalae* species group is difficult to work with taxonomically because, unlike the related Hawaiian *Drosophila* species groups, very few characters exist that define species or aggregates of species (*e.g.,* the *split tarsus* subgroup of the *modified tarsus* species group; Hardy & Kaneshiro(1979)). This is probably due to the fact that, like the closely related genus *Scaptomyza*, these species have relatively simple mating behaviors (Spieth, 1966). This tends to reduce the role of sexual selection in the generation of sexual dimorphism and other morphological differentiation. The placement of the *haleakalae* group as basal within the Hawaiian *Drosophila* (Throckmorton, 1966), close to the divergence of the genus *Scaptomyza*, suggests that extensive sexual dimorphism observed in more derived Hawaiian drosophilid taxa evolved after the divergence of the *haleakalae* group. Based on this phylogenetic position, it is clear that widespread sexual dimorphism, and the fascinating mating behaviors which characterize the majority of Hawaiian *Drosophila*, evolved after the divergence of the *haleakalae* species group.

The taxonomic framework proposed by Hardy *et al*. (2001) was based on only a few key morphological characteristics and was intended to be a working hypothesis of relationships within this difficult to characterize group, rather than a formal phylogenetic hypothesis. The work of Bonacum (2001) improved on this framework, generating phylogenetic support for the *fungiperda* complex (Fig. 2, A: *D. fungiperda* & *D. nigella*) and *venusta* cluster (Fig. 2, C: *D. inciliata* & *D. longiperda*). His results also call into question the monophyly of the *cilifemorata* subgroup. This heterogeneous clade contains a number of species (Table 1), including *D. nigra*, which is strongly supported as the sister of the *fungiperda* complex (of the *haleakalae* subgroup) rather than a member of the *cilifemorata* subgroup (Figure 2, B). The present study further expands on the previous work by sampling multiple individuals from 4 of the 5 proposed subgroups and including 87 morphological and behavioral characters and over 5000 base pairs of rapidly evolving molecular characters. This study is able to provide significant support for 14 of the 17 nodes in the ingroup (compared to 3 of 12 in the previous phylogenetic work (Bonacum, 2001)). As such, we are now able to propose a phylogenetic framework of relationships within the *haleakalae* species group. Table 5 summarizes the changes we propose.

In spite of strong support for the monophyly of the *haleakalae* species group (node 17; Fig. 4, BP & JK = 100, DI = 66; Fig. 5, BP = 100), it is clear that 2 of the subgroups proposed in Hardy *et al.* (2001), *scitula* and *cilifemorata*, are polyphyletic. Some of the taxa initially placed in these subgroups clearly belong to other clades and will be removed. For example, *D. insignita* (*cilifemorata* subgroup, *insignita* complex) is nested within a clade of species placed in the *polita* subgroup (node 11; Fig. 4, BP & JK = 100, DI = 13; Fig. 5, BP = 100). We propose that *D. insignita* be removed from the *cilifemorata* subgroup and be placed in the *polita* subgroup (Table 5). Two closely related taxa, *D. chicae* and *D. curtitarsis*, were not sampled in our study but have also been transferred to the *polita* subgroup, although their exact placement will hinge upon future phylogenetic work. Likewise, it is clear that *D. nigra* (*cilifemorata* subgroup, *cilifemorata* cluster) should be considered

Table 4. Comparison of Individual and Combined Analyses.

Node[1]	MP&ML[2]	DI[3]	Individual Search[4]	Positive PBS[5]	Negative PBS[6]
1	++	5	**COII** [4], **ITS** [0]	l(2)not [4], snf [2]	indels [-1], Marf [-4]
2	++	2	**Marf** [2]	l(2)not [5], snf [2]	COII [-3], ITS [-2], morph [-2]
3	++	7	**ITS** [5]	COII [1], sia [1], l(2)not [2], snf [2]	glass [-1], Marf [-3]
4	ML	na	**l(2)not**		
5	++	12	**COII** [9], **ITS** [2], ***l(2)not*** [2], ***Marf*** [0], morph [2]	snf [2]	sia [-1], glass [-4]
6	++	4	***l(2)not*** [6], snf [2]		COII [-2], Marf [-2]
7	ML	na			
8	ML	na	**Marf**		
9	++	5	***Marf*** [7]	morph [2]	ITS [-2], indels [-2]
10	++	18	COII [9], glass [0], **ITS** [2], ***Marf*** [2], indels [5]		l(2)not [-1]
11	++	13	**ITS** [7], ***Marf*** [2], indels [2]	COII [5], snf [1]	l(2)not [-4]
12	ML	na	COII, ITS		
13	++	7	glass [0], **ITS** [2], Marf [6]	l[2]not [2], snf [2], morph [4]	COII [-8], indels [-1]
14	ML	na	**ITS**		
15	ML	na	**ITS**		
16	++	8	***Marf*** [4], morph [0], indels [1]	sia [3], **ITS** [4]	COII [–2], glass [-1], snf [-1]
17	++	66	COII [0], sia [2], glass [0], **ITS** [11], ***l(2)not*** [14], ***Marf*** [27], indels [4], morph [9], ***snf*** [-1]		
18	MP	3	snf [1], morph [3], **ITS**	sia [1], Marf [1]	COII [-2], l(2)not [-1]
19	MP	2	l(2)not [1], snf [2],	Marf [1]	COII [-2]
20	MP	1	l(2)not [0]	sia [2], ITS [2], snf [3]	COII [-2], Marf [-1], indels [-1], morph [-2]

1. Node recovered in either combined MP or ML analyses (see Figs. 4, 5).
2. Relationship is present in combined MP, ML, or both (++) analyses.
3. Decay index (DI) in combined MP tree. Nodes only found in ML analyses have no DI.
4. Individual partition search in which specified node is present, along with partitioned branch support from the combined MP analysis in [ ]. Taxa in bold also appear in individual ML analyses. Bold, underlined partitions are present in individual ML and combined ML analysis but not present in MP searches.
5. Partitions contributing positive support to relationship in combined MP analysis, but not supporting node in individual analyses.
6. Partitions contributing negative support to relationship in combined MP analysis, but not supporting node in individual analyses.

a member of the *fungiperda* complex (node 18; Fig. 4, BP = 82, JK = 84, DI = 3; node 6; Fig. 5, BP = 68). All 3 of these species (*D. nigra, D. fungiperda, D. nigella*) lack a rimmed labellum and it is clear based on both morphological and molecular characters that they form a clade (Figs. 3–5).

Drosophila iki, another species initially placed in the *cilifemorata* cluster, should be removed to the newly erected *iki* complex within the *haleakalae* subgroup (Table 5) with 2 other species, *D. multiciliata* and *D. paraanthrax* (node 13; Fig. 4; BP = 96, JK = 98, DI = 7; Fig. 5, BP = 97). It is clear that the remaining taxa in the *cilifemorata* subgroup, *D. dolichotarsis* and *D. longiperda*, are closely related to the *haleakalae* subgroup (node 3; Fig. 4, BP = 89, JK = 93, DI = 7; Fig. 5, BP = 94). We suggest placing the remaining complexes and clusters of the *cilifemorata* subgroup into the *haleakalae* subgroup until additional taxon sampling can be undertaken (Table 5). This placement, while greatly increasing the size of the *haleakalae* subgroup, reflects our current understanding of phylogenetic relationships within the *haleakalae* species group.

The transfer of *D. multiciliata* to the *iki* cluster means that *D. melanosoma*, the only remaining member of the *anthrax* subgroup sampled (Table 5) is basal to all the remaining *haleakalae* group species (node 16; Fig. 4, BP = 80, JK = 91, DI = 8; Fig. 5, BP = 78). This relationship was suggested by Hardy *et al.* (2001) but should be tested by sampling additional taxa. The transfer of *D. paraanthrax* to the *iki* cluster, along with the transfer of *D. insignita* to the *polita* complex (Table 5), renders the *polita* complex monophyletic (node 11; Figs. 4, 5).

The 3 members of the *scitula* subgroup that we sampled in this study are also not monophyletic. One, *D. fulgida*, should be placed in the *fungiperda* complex of the *haleakalae* subgroup based on both the MP (Fig. 4; BP = 72, JK = 81, DI = 4) and ML (Fig. 5; BP = 68) analyses. The placement of *D. melanosoma* and *D. scitula* is somewhat more problematic and represents 2 of the more poorly supported clades in either phylogeny (Figs. 4, 5). *Drosophila melanosoma* has some affinities with the *haleakalae* subgroup, although it is not firmly allied with any one subgroup. *Drosophila scitula* is either basal to the *polita* subgroup (Fig. 4) or basal to all but the *anthrax* subgroup (Fig. 5). These 2 species, along with the remaining members of the *scitula* subgroup, *D. setositibia* and *D. subopaca*, should remain as unplaced in the *haleakalae* species group until additional work is done to more firmly assess their phylogenetic location (Table 5).

Divergence Times and Biogeographic Patterns

We are interested in estimating the divergence times of the major lineages within the *haleakalae* species group, as well as the age of the group as a whole in order to better understand the evolutionary dynamics that have shaped this group and other clades of Hawaiian *Drosophila*. Three calibration points (see Materials and Methods) were used to estimate divergence dates with a local molecular clock (Yoder & Yang, 2000). Because of heterogeneity within the *fungiperda* complex (above), we discarded this calibration point and used the mean divergence between *D. haleakalae-D. ochropleura* (node 1; 0.5–1.9 MY) and *D. bipolita-D. canipolita-D. insignita* (node 10; 3.7 MY). Ranges shown in Figure 6 are means from the local clocks specified by the TREE 1 and TREE 2 constraints.

Based on our estimates, the *haleakalae* species group diverged from the picture wing species group 20–21 MY ago. This is in agreement with the age estimates for the origin of the Hawaiian *Drosophila* at 26 MY (DeSalle, 1992; Russo *et al.*, 1995) and the placement of the *haleakalae* group as basal in the Hawaiian *Drosophila* radiation (Baker & DeSalle, 1997; Bonacum, 2001; O'Grady, 2002; Throckmorton, 1966). However, at that point in time little high elevation rainforest, the habitat required by all Hawaiian *Drosophila*, existed (Price & Clague, 2002). It is interesting to note that the major diversification of the *haleakalae* species group did not occur until about 10 MY ago (Fig. 6), when more suitable habitat was present on Gardner Pinnacles, La Perouse, and Necker Islands (Price & Clague, 2002). This pattern might suggest either evolutionary stasis or extensive extinction at the base of this lineage 20–10 MY ago. It might also be that sampling additional taxa within the basal *anthrax* subgroup could move the age of this group back to perhaps 15 MY, when large amounts of rainforest habitat was present on what is now Gardner Pinnacles (Price & Clague, 2002).

The ages of the major, well supported lineages within the *haleakalae* species group are all very similar, between 4.0 and 6.3 MY (Fig. 6). These groups are all quite recent, on the order of the age

Table 5. Revision of phylogenetic relationships in the *Drosophila haleakalae* species group.

ID	Taxon	Hardy *et al.*, 2001	Current Study
I.	*anthrax* subgroup	*anthrax, demipolita, fascigera, fuscifrons, hemianthrax,* ***melanoloma****,* ***multiciliata****, nigropolita, retrusa, seorsa*	*anthrax, demipolita, fascigera, fuscifrons, hemianthrax,* ***melanoloma****, nigropolita, retrusa, seorsa*
II.	*cilifemorata* subgroup	*inciliata,* ***longiperda****, tanytarsis, venusta, cilifemorata,* ***dolichotarsis****, flaviceps,* ***iki****,* ***nigra****, stenoptera, swezeyi, denotata, sabroskyi, insignita*	This subgroup is not monophyletic. While it was possible to removed some one taxon (*insignita*) and place it in the *polita* subgroup, the majority of species here are actually closely related to several different *haleakalae* subgroup clades and will be considered as part of the *haleakalae* subgroup.
III.	*haleakalae* subgroup	*atrifacies, brunneicrus,* ***ochropleura****,* ***fungiperda****,* ***nigella****, clara, cryptica,* ***haleakalae****, macrochaetae*	We recognize several clades within this subgroup: (1) *fungiperda* complex: ***fungiperda****,* ***nigella****,* ***nigra, fulgida*** (2) *haleakalae* complex: *clara, cryptica,* ***haleakalae****, macrochaetae* (3) *brunneicrus* complex: *brunneicrus,* ***ochropleura*** (4) *atrifacies* complex: *atrifacies* (5) *venusta* cluster: *inciliata,* ***longiperda****, tanytarsis, venusta* (6) *cilifemorata* cluster: *cilifemorata,* ***dolichotarsis****, flaviceps, stenoptera, swezeyi, chicae, curtitarsis* (7) *iki* complex: ***iki, multiciliata, paraanthrax*** (8) *denotata* complex: *denotata, sabroskyi*
IV.	*luteola* subgroup	*fuscoapex, tamashiroi, luteola, quinqueramosa*	*fuscoapex, tamashiroi, luteola, quinqueramosa*
V.	*polita* subgroup	***bipolita****,* ***canipolita****, dives, flavisternum, illusiopolita, lissodora, mecocnemia,* ***paraanthrax****,* ***polita****, pretiosa*	***bipolita, canipolita****, dives, flavisternum, illusiopolita,* ***insignita****, lissodora, mecocnemia,* ***polita****, pretiosa, chicae, curtitarsis*
VI.	*scitula* subgroup	***fulgida, melanosoma, scitula****, setositibia, subopaca*	This subgroup is not monophyletic. The species sampled have various affinities, none of which are strongly supported. With the exception of *fulgida*, the placement of these species should be considered tentative pending additional work.
VII.	placement uncertain	n/a	***melanosoma, scitula****, setositibia, subopaca*

Species in **bold** were sampled in the current study.

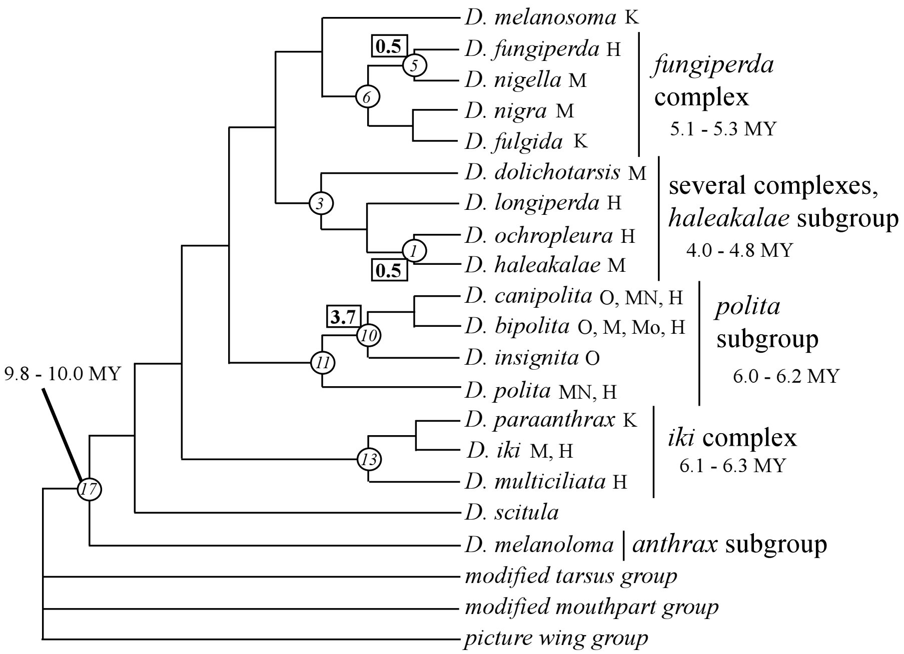

Figure 6. Chronogram showing results of local molecular clock analyses (Yoder & Yang, 2000) based on ML tree topology. Calibration points are in squares and estimated divergence times are placed at various nodes. All ages are in millions of years (MY). Distribution of terminal taxa as follows: K = Kaua'i; O = O'ahu; M = Maui, MN = Maui Nui, Mo = Moloka'i; H = Hawai'i. Revised groupings of species, after Table 5, are also shown. Outgroups have been collapsed into a polytomy.

of the oldest existing high island with suitable rainforest habitat, Kaua'i (5.1 MY). The ages of the internodes connecting these lineages (i.e., nodes 8, 14, 15, 16; Fig. 5) were not estimated because they are very short and poorly supported in the various phylogenetic analyses we have performed (Fig. 4, 5). This suggests that a bottleneck (extinctions or low rates of speciation) prior to the formation of the present day Hawaiian Islands may have taken place in the *haleakalae* species group, as has been suggested in other Hawaiian taxa (Price & Clague, 2002). Such a bottleneck may have been followed by a burst of speciation, giving rise to the present day *haleakalae* group taxa. Additional studies on this and other clades of Hawaiian *Drosophila* will be needed to verify if this pattern is general within this lineage.

One pattern that is not observed in the present data set is the linear progression of taxa found on older high islands to those endemic to younger islands (Bonacum *et al.*, *in press*; Hormiga *et al.*, 2003; Jordan *et al.*, 2003). This is partially due to that fact that taxa in the *haleakalae* species group are reliant on restricted, ephemeral host substrates (fungi) and are quite rare and difficult to sample, making full representation difficult. The other factor is that the taxonomy of this group is difficult to resolve due to few morphological changes between closely related taxa. For example, Hardy *et al.* (2001) listed 16 taxa that were present on multiple islands. This is a rare phenomenon in other Hawaiian groups because of a multitude of sexually selected characters that rapidly change from island to island. Clearly, further genetic studies will be required to better understand the evolutionary forces acting on this and other Hawaiian *Drosophila* groups.

On Hybridization and Gene Choice in Insect Molecular Systematics

Several authors have pointed out problems with using molecular characters to infer phylogenetic relationships when the potential for natural hybridization exists (e.g., Maddison, 1997). In such cases, differential transfer of genetic material can yield incongruent gene trees and combined analysis may result in a biased estimate of species phylogeny. It is unclear whether this may be the case in the *haleakalae* species group as studies of natural hybridization within this group are completely lacking (Kaneshiro and colleagues [Carson *et al.,* 1989; Kaneshiro & Val, 1977; Kaneshiro, 1990] have examined this in other Hawaiian *Drosophila* groups). Furthermore, the individual gene trees obtained here, while not in complete agreement, are not significantly different from one another so it is difficult to tease apart difference due to common ancestry, introgression, or stochastic effects of nucleotide substitution. Further studies within the Hawaiian *Drosophila* examining migration and gene flow within and between populations (and closely related species) are sorely needed before we can adequately address this question. What is clear at this time is that hybridization between closely related taxa, either in the past or in the present day, can obfuscate phylogenetic inference with both molecular and morphological characters.

Molecular systematists working on insects have relied on a standard set of genes, most of which were developed based on previous genetic work in *Drosophila melanogaster*. Gene choice in the past has been driven, at least in part, by what working primers were available, rather than what genes were evolving at the appropriate rate to be potentially informative at the phylogenetic level being examined. A previous study employing *Adh*, *Gpdh*, and 16S (Bonacum, 2001), 3 relatively slowly evolving loci have been widely used in insect systematics, was not particularly effective in resolving relationships among the closely related *haleakalae* group species. Based on some preliminary studies (Zilversmit *et al.*, 2002a), we identified several loci that were evolving rapidly enough to be of use for species-level problems.

This study represents the first application of 5 nuclear genes *Marf, Rpt4, sia, glass,* and *l(2)not-1* to species-level phylogenetic problems. We used 2 criteria, (1) the number of parsimony informative characters and (2) the presence of highly variable, rapidly evolving regions to select loci to resolve relationships among closely related species. The two most influential loci in this study were the *Marf* and *l(2)not*. Both added a significant amount of support to the *haleakalae* phylogeny (Table 4). It is interesting to note that, unlike the slowly evolving *Adh* and *Gpdh* genes, both these protein coding loci do not code for enzymes (*Marf* is a GTP binding protein and *l(2)not* is an integral membrane protein found in membranes of the endoplasmic reticulum). Thus, the gene products of *Marf* and *l(2)not* may be effected by distinctly different selective pressures and, as a result, evolve much more rapidly than enzymatic loci. Homologs of *Marf* and *l(2)not* are present in a wide diversity of Metazoa, suggesting that they may be useful in inferring phylogenetic relationships outside of the Drosophilidae.

Acknowledgments

The authors thank J. Bonacum, R. DeSalle, F. C. do Val, D. Oliveira, C. Specht, and J. Stark for helpful discussions. We would also like to gratefully acknowledge the following organizations and individuals for granting us collection permits: East Maui Irrigation (Garret Hew), The Nature Conservancy, Hawaii (O‘ahu – Trae Menard; Moloka‘i – Tina Lau), Division of Land and Natural Resources, Kaua‘i (Ed Petteys), United States Army (Makua Valley, O‘ahu), and Hawaii Volcano National Park (David Foote, Darcy Hu). Steve Montgomery, Michael Kambysellis, and Elysse Craddock provided assistance in the field. The work was supported by NSF DEB 01-29105 to R. DeSalle and P. O’Grady.

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Insects Associated with Fruits of the Oleaceae (Asteridae, Lamiales) in Kenya, with Special Reference to the Tephritidae (Diptera)

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Abstract

Collections of fruits from indigenous species of Oleaceae were made in Kenya between 1999 and 2003. Members of the four Kenyan genera were sampled in coastal and highland forest habitats, and at altitudes from sea level to 2979 m. *Schrebera alata*, whose fruit is a woody capsule, produced Lepidoptera only, as did the fleshy fruits of *Jasminum* species. Tephritid fruit flies were reared only from fruits of the oleaceous subtribe Oleinae, including *Olea* and *Chionanthus*. Four tephritid species were reared from *Olea*. The olive fly, *Bactrocera oleae,* was found exclusively in fruits of *O. europaea* ssp. *cuspidata,* a close relative of the commercial olive, *Olea europaea* ssp. *europaea*. Olive fly was reared from 90% (n = 21) of samples of this species, on both sides of the Rift Valley and at elevations to 2801 m. *Bactrocera munroi*, **sp. nov**. was reared from both *O. europaea* ssp. *cuspidata* and *Olea welwitschii*. *B. munroi* is only the second *Bactrocera* species to be reared from *O. europaea* s.l. *Bactrocera biguttula* and *Ceratitis capitata* were reared from the coastal olive, *Olea woodiana* ssp. *disjuncta*. A new species of adramine tephritid, *Munromyia whartoni* **sp. nov**., was reared from *Chionanthus niloticus* in western Kenya. Opiine braconid parasitoids were reared from *M. whartoni* and *B. oleae*. The former was attacked by a single species of *Psyttalia*, while the latter was parasitized by *Psyttalia concolor*, *Psyttalia lounsburyi* and *Utetes africanus*. In some collections, rates of parasitization of olive fly by *P. lounsburyi* exceeded 30%. Moths and several of their parasitoids were reared from all four genera of Oleaceae. Species richness of moths in oleaceous fruits was about twice that of tephritids.

The subgenus *Afrodacus* Bezzi is proposed as a new synonym of subgenus *Daculus* Speiser, and all Asian species previously placed in subgenus *Afrodacus* are transferred to subgenus *Bactrocera*. Descriptions of 2 new species of Tephritidae, a key to the species of *Munromyia*, and a synopsis (with key to species) of African *Bactrocera* subgenus *Daculus* are provided.

Introduction

The family Oleaceae, although concentrated primarily in southeast Asia and Australasia, is found in diverse tropical and temperate regions of the world and has a nearly cosmopolitan distribution (Heywood, 1998). Recently, Wallander & Albert (2000) used chloroplast DNA sequences from species representing all known oleaceous genera to construct a phylogeny of the family. They rejected a subfamilial classification (e.g., Johnson, 1957) of the Oleaceae after showing that the Jasminoideae were paraphyletic. Instead they proposed a tribe-based higher classification and it is their interpretation of Oleaceae phylogeny that we follow in this paper.

In Kenya, the family is poorly represented, having only 4 of the 25 currently recognized genera. Three of the indigenous genera (*Olea* L. and *Chionanthus* L. [Oleeae: Oleinae] and *Jasminum* L. [Jasmineae]) have representatives that are widely distributed in Kenya: from coastal lowlands to western highlands and at altitudes from sea level to ca. 3000 m, primarily in woodland (*sensu* Greenway, 1973) and forest habitats (Beentje, 1994). The other Kenyan genus, *Schrebera* Roxb. (Oleeae: Schreberinae), is represented by a single species and confined to upland dry forest (Beentje, 1994). While *Schrebera alata* (Hochst.) Welw. produces a dry capsule, *Chionanthus* (drupe), *Olea* (drupe), and *Jasminum* (berry) all produce fleshy fruits. The genus *Olea* has recently been revised (Green, 2002) and we follow this classification.

Among the oleaceous plants, only cultivars of *Olea europaea* L. ssp. *europaea* produce economically important fruits. It is the source of edible olives and olive oil and a major commercial crop in subtropical areas of the world with a Mediterranean climate, particularly in southern Europe and the Levant. Commercial olives are also cultivated extensively in South Africa and California. Commercial olive is thought to be derived from *Olea europaea* L. ssp. *cuspidata* (Wall ex G. Don) (Mabberly, 1998). The similarity of *Olea europaea* L. ssp. *africana* (Mill.) P. S. Green, the other previously recognized indigenous sub-Saharan member of *O. europaea*, to *O. europaea* ssp. *cuspidata* has long been recognized, and recently they have been placed in synonymy (Green, 2002), with *O. europaea* ssp. *cuspidata* having priority.

In many parts of Mediterranean Africa and Europe, *Bactrocera oleae* (Rossi) is the most important pest of cultivated olives (Mustafa & Al-Zaghal, 1987), and efforts to find natural enemies of *B. oleae* span nearly a century (Silvestri, 1913; Raspi, 1993; Purcell, 1998). Several species of parasitic wasps have been introduced into southern Europe in an effort to control *B. oleae* (Silvestri, 1913; Greathead, 1976; Wharton, 1989). Of these, a measure of success has been seen only with *Psyttalia concolor* (Szépligeti) which became established, but in low densities, following its release in Italy before and after World War I (Monastero, 1931; Silvestri, 1939; Raspi, 1993). Augmentative releases of laboratory-reared *P. concolor* have been used for more than 50 years to help control populations of *B. oleae* (Raspi, 1993; Raspi & Loni, 1994; Kennett *et al*., 1999). Yet olive losses continue to plague growers (Raspi *et al.*, 1996), and introductions of *P. concolor* have failed in several other regions of Europe (Clausen, 1978; Loni, 1997), possibly due, at least in part, to climatic factors (Raspi & Loni, 1994).

Bactrocera oleae occurs widely throughout eastern and southern Africa, attacking fruits of *O. europaea* ssp. *cuspidata*, and the potential benefit of exploration in sub-Saharan Africa for natural enemies of *B. oleae* has long been recognized (Silvestri, 1913, 1914, 1916). Silvestri collected 14 species of parasitic wasps from fruits infested with *B. oleae* in Eritrea in 1914, and returned to Italy with 10 of them. Although none of these became established after release (Neuenschwander, 1982; Wharton, 1989), *P. concolor*, as noted above, was repeatedly released and eventually became established. With the realization that neither native natural enemies nor *P. concolor* was providing satisfactory control in most areas, interest in obtaining new natural enemies was revived in the 1970s. A single expedition to Ethiopia and Kenya was made in 1975 by Greathead (1976) to collect parasitoids of olive fly. However, no fruiting specimens of *Olea* species were encountered in Kenya and searches in Ethiopia produced meager results. Neuenschwander (1982) was much more successful in his search for olive fly parasitoids in South Africa, but unfortunately the material shipped to Europe could not be cultured and thus no species were established.

In this paper we report on the insects reared from oleaceous fruits collected during a widespread survey of insects of wild fruits of Kenya conducted from 1999 to 2003. We focus special attention on the tephritids and their parasitoids recovered from native olive species, given the recent introduction of olive fly to California and the concomitant interest in reviving a classical biological control program for this pest (Collier & Van Steenwyk, 2003).

Materials and Methods

For the overall survey of indigenous fruits, sites were chosen to ensure extensive sampling of major woodland and forest habitats both east of the Gregory Rift Valley (coastal forests, mid-altitude for-

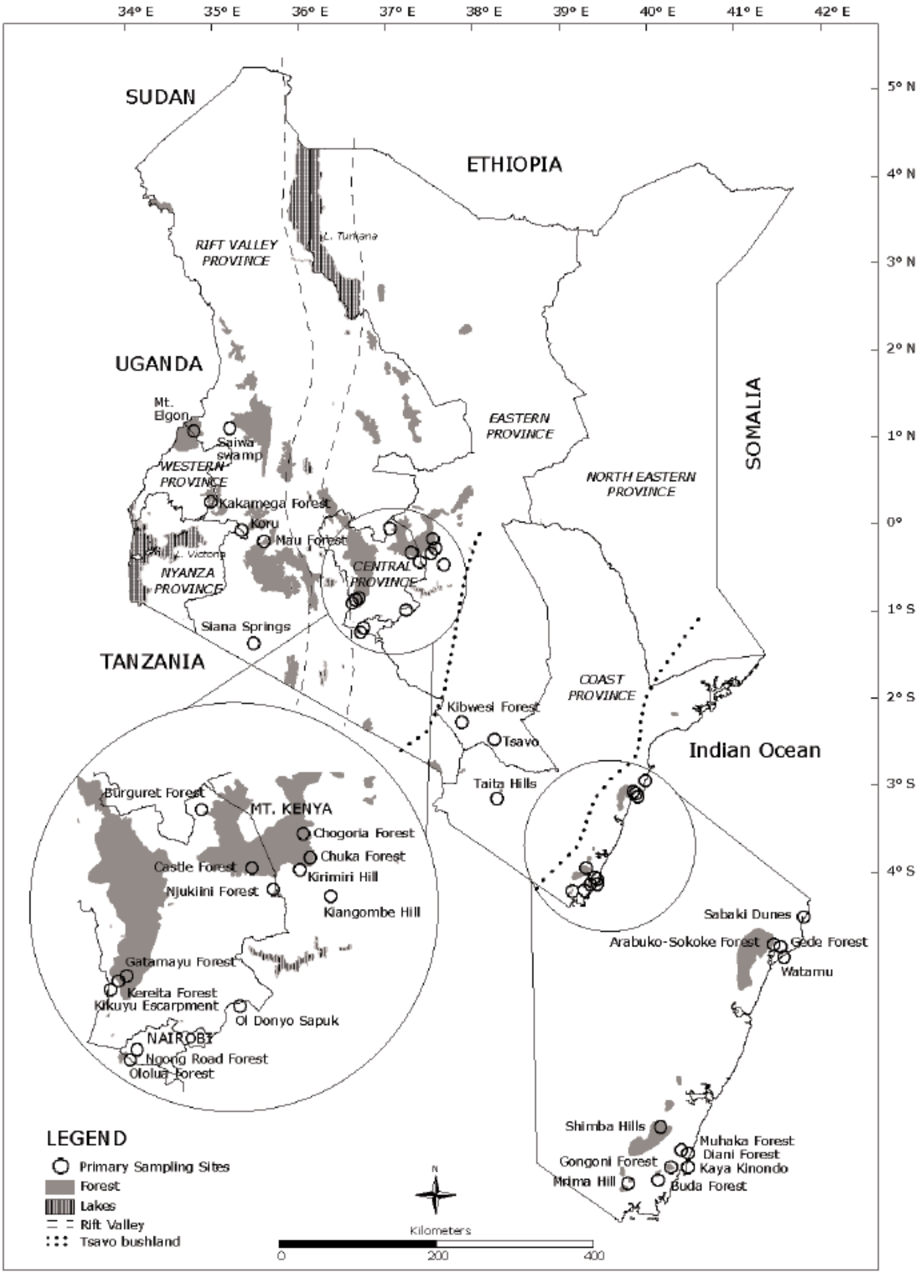

Figure 1. Collecting sites in Kenya.

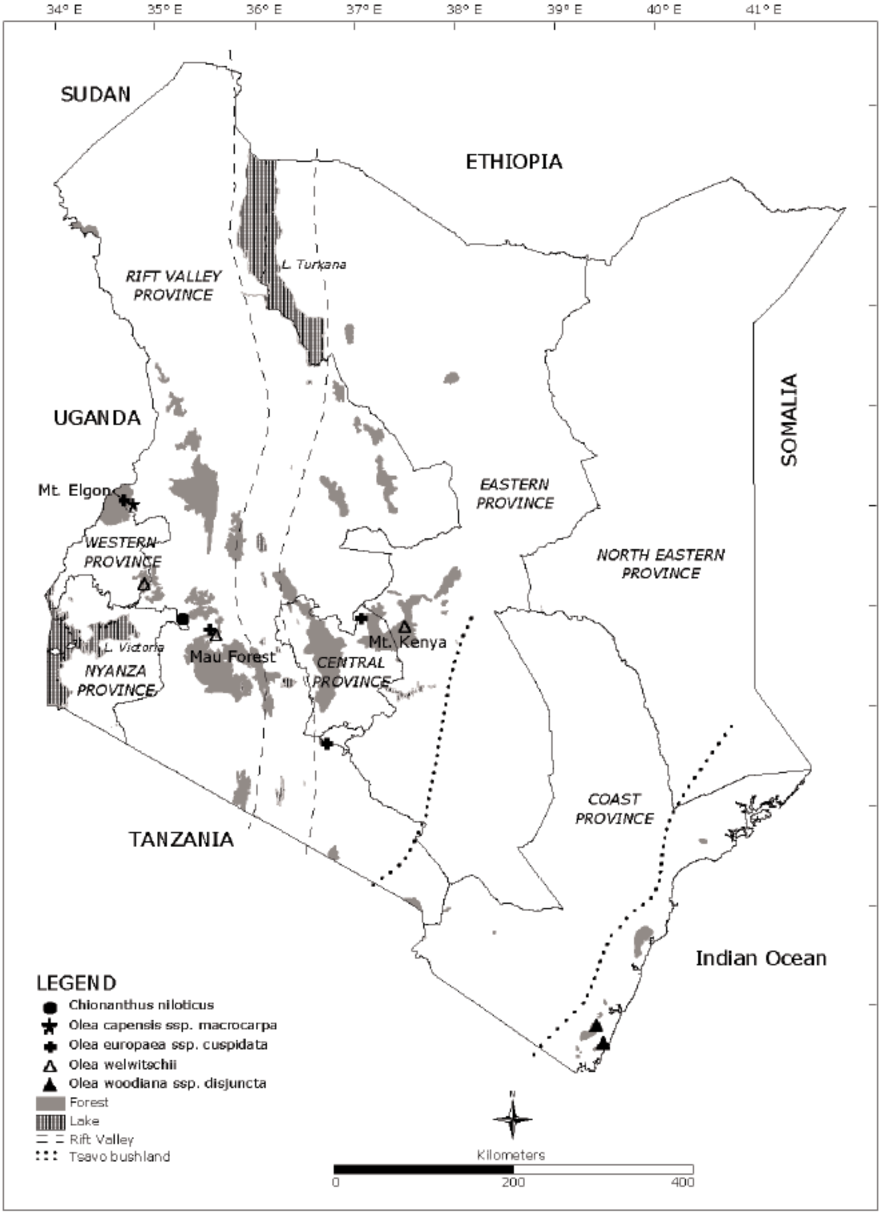

Figure 2. Collection locations of *C. niloticus* and *Olea* species in Kenya.

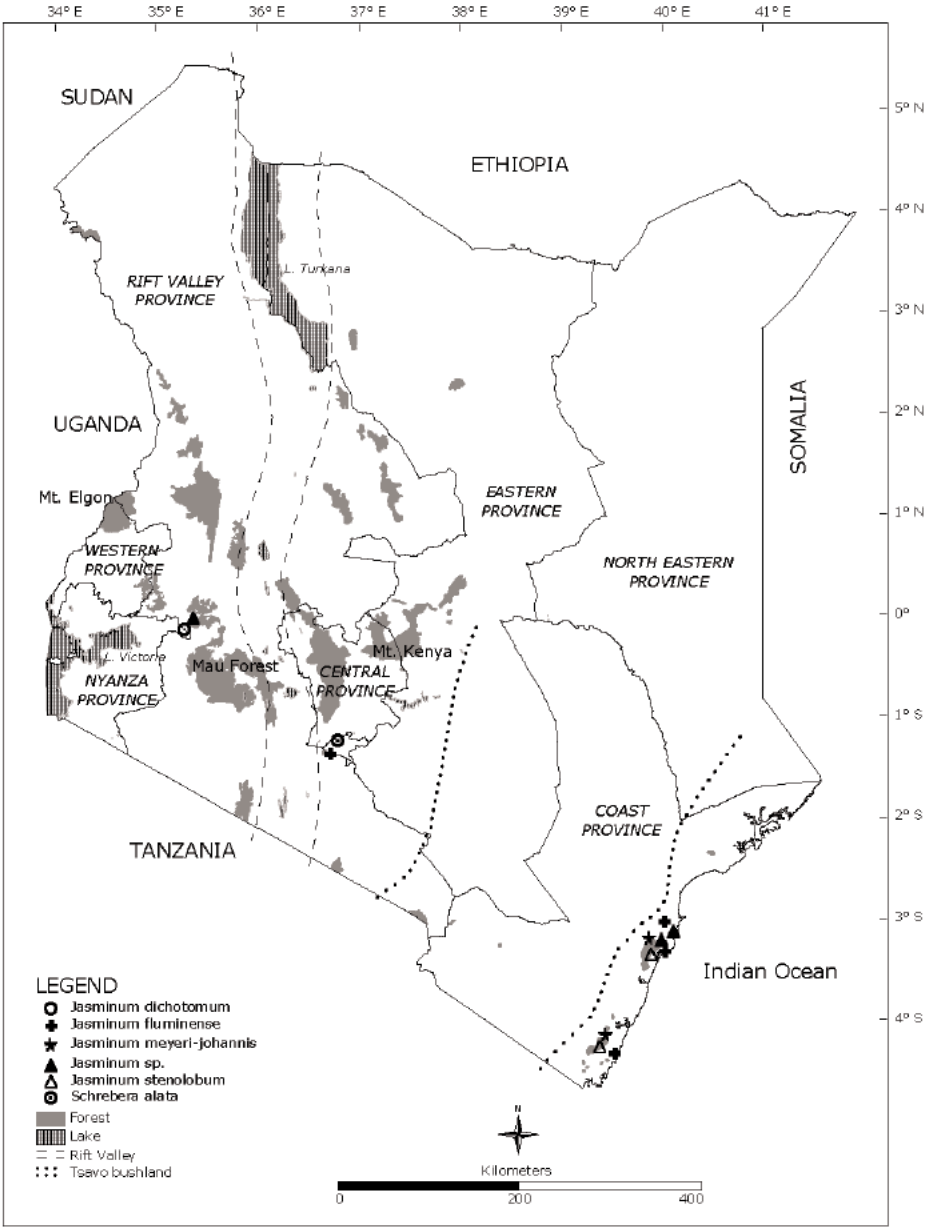

Figure 3. Collection locations of *Jasminum* species and *Schrebera alata* in Kenya.

Table 1. Collections of Oleaceae[1]

Tribe	Subtribe	Plant species	No. of collections	No. of fruits collected	Total weight (gm)	Months collected	Region collected[2]	Altitudinal range (m)
Jasmineae		*Jasminum dichotomum* Vahl	3	315	130	1,2	we	1460–1565
		Jasminum fluminense Vell.	5	918	239	1,4,8,10,11	ce,co	24–1750
		Jasminum meyeri-johannis Engl.	3	1,260	631	7,8	co	55–270
		Jasminum L. sp.	3	494	197	7,8,9	co,we	10–1574
		Jasminum stenolobum Rolfe	2	1,049	520	4,7	co	55–436
Oleeae	Oleinae	*Chionanthus niloticus* (Oliv.) Stearn	3	1,958	1,325	6,7,8	we	1565
		Olea capensis L. ssp. *macrocarpa* (C. H. Wright) I. Verd.	1	155	123	2	we	2234
		Olea europaea L ssp. *cuspidata* (G. Don.) Cif.	21	28,625	7,312	1,2,3,4,5,8,9,11	ce,we	1706–2979
		Olea welwitschii (Knobl.) Gilg & Schnellenb.	8	7,287	2,921	6,8,9	ce,we	1550–2448
		Olea woodiana Knobl. ssp. *disjuncta* P. S. Green	2	758	424	7,8	co	5–201
	Schreberinae	*Schrebera alata* Welw.	2	167	316	4	ce	1759–1889
		Totals	53	42,986	14,138			

1. Higher classification based on Wallander & Albert (2000).

2. ce = central highlands, co = coastal lowlands, we = western highlands.

est, high altitude dry and wet forest), and west of it (high altitude wet forest). Sites included those reported earlier (Copeland *et al.*, 2002) with some important additions (Fig. 1). Central highland forests are separated by the Gregory Rift Valley from forests of the western highlands, while coastal forests are isolated from both by a broad swath of xeric "Tsavo bushland" (Lind & Morrison, 1974) [= "dry scrub with trees", (Greenway, 1974)] (Fig. 1). In addition to forests, fruits were sampled in other habitats, particularly open woodland in highland areas, and shrubland, dune, coral-rag associations, and open woodland at the coast. GPS data were recorded at the site of each collection or at the nearest opening if the fruits were collected in dense forest.

Monthly collections were made from February 1999 through January 2003 at sites in western, central, and eastern Kenya. Details of the collection and handling of fruit samples are provided in Copeland *et al.* (2002). Additionally, in order to determine whether differences in developmental stages of fruit influenced the infestation rate in olives, we made matched collections of ripe and green fruits at 2 separate locations (1960 m and 1974 m) in Burguret Forest on the western side of Mount Kenya (Table 2).

Specimens of each plant from which fruits were collected were pressed in the field. Additionally, photographs were taken of representative fruits from all samples. Plant specimens and, sometimes, fruit photographs were used for identification at the East African Herbarium. For the occasional cases when fallen fruits were sampled under trees from which it was impossible to collect a specimen, plant identification was made with reference to published (Beentje, 1994; Agnew & Agnew, 1994) and unpublished lists of local flora, using fruit, bark, and leaf characters, the latter observed with binoculars.

We are grateful to the curators of the following institutions for providing tephritid specimens to IMW and RSC: BMNH = The Natural History Museum, London, UK (J.E. Chainey); MSNM = Museo Civico di Storia Naturale, Milan, Italy (F. Rigato); MRAC = Koninklijk Museum voor Midden Afrika, Tervuren, Belgium (M. De Meyer & E. De Coninck); NMKE = National Museums of Kenya, Nairobi, Kenya (W. Kinuthia); USNM = National Museum of Natural History, Washington D. C., USA (A. Norrbom); SANC = National Collection of Insects, Plant Protection Research Institute, Pretoria, South Africa (M.W. Mansell).

Results

Distribution of Oleaceous Fruit Samples

Species of Oleaceae were collected throughout the forested and woodland areas of southern Kenya. A summary of the 53 fruit samples collected from these plants is given in Table 1. The distributions of collections of Oleeae: Oleinae (four *Olea* species and *Chionanthus niloticus* (Oliv.) Stearn) are shown in Fig. 2. *Olea woodiana* Knobl. ssp. *disjuncta* P. S. Green is a coastal lowland forest species (Beentje, 1994; as *Olea woodiana* Knobl.) and was collected at 2 sites on the Kenyan south coast. The remaining four species were collected in high altitude forest in central and western Kenya. Ripe fruits of *O. europaea* ssp. *cuspidata* were sampled at an altitude of 2979 m on Mt. Elgon, western Kenya, ca. 600 m higher than that previously recorded for herbarium specimens of this species (Beentje, 1994). *Olea europaea* ssp. *cuspidata* was also found in mid-altitude woodland (Kibwesi Forest, Eastern Province Kenya, 1015 m, Fig. 1) growing on volcanic soil. However, we did not find ripe fruits at this site. Species of *Jasminum* were collected at various coastal and upland sites, while *Schrebera alata* was found only at 2 sites in highland forest in central Kenya (Fig. 3).

Insects Associated with Oleaceae

Tephritidae and their parasitoids

Tephritidae and their parasitoids were reared from fruits of Oleeae: Oleinae, represented by *Chionanthus niloticus* and 3 of the *Olea* species (Tables 2 and 3). Neither fruit flies nor their parasitoids were recovered from Oleeae: Schreberinae (*Schrebera alata)* or Jasmineae (*Jasminum* species), although fruits of these species were attacked by lepidopteran larvae (see next section). Similarly, tephritids were not recovered from the single collection we made of *O. capensis* ssp. *macrocarpa*.

Table 2. Distribution and fruit infestation indices of tephritid-positive Oleaceae species.[1]

Plant species[2]	Region[3]	Location	Altitude (m)	Sampling date	No. of fruits	Weight (gms)	*B. biguttula* per 1000 fruit (per kg)	*B. oleae* per 1000 fruit (per kg)	*B. munroi* per 1000 fruit (per kg)	*M. whartoni* per 1000 fruit (per kg)
Chionanthus niloticus	we	Koru; Brooks' farm	1565	6/4/00	1035	905	0 (0)	0 (0)	0 (0)	47 (54)
			1565	7/15/00	515	210	0 (0)	0 (0)	0 (0)	161 (395)
			1565	8/17/00	408	210	0 (0)	0 (0)	0 (0)	429 (833)
Olea europaea ssp *cuspidata*	ce	Ololua Forest	1706	2/3/00	539	110	0 (0)	18 (91)	0 (0)	0 (0)
			1823	2/23/00	nd[4]	nd[4]	0 (0)	nd[4]	0 (0)	0 (0)
			1750	2/23/00	nd[4]	nd[4]	0 (0)	nd[4]	0 (0)	0 (0)
			1823	3/26/00	775	169	0 (0)	330 (1515)	0 (0)	0 (0)
			1823	4/8/00	191	40	0 (0)	84 (400)	0 (0)	0 (0)
			1823	4/8/00	363	76	0 (0)	157 (750)	0 (0)	0 (0)
			1823	4/21/00	203	42	0 (0)	108 (524)	0 (0)	0 (0)
			1823	4/28/00	nd[4]	nd[4]	0 (0)	nd[4]	0 (0)	0 (0)
	ce	Burguret Forest	1961	5/17/02	661	134	0 (0)	0 (0)	0 (0)	0 (0)
			1974	8/15/02	2942	691	0 (0)	85 (360)	0 (0)	0 (0)
			1960	8/16/02	2235	535	0 (0)	174 (725)	0 (0)	0 (0)
			2062	9/21/02	5000	1106	0 (0)	75 (338)	0 (0)	0 (0)
			2010	11/13/02	1000	220	0 (0)	4 (18)	6 (27)	0 (0)
	we	Mau Forest	2187	9/19/00	235	47	0 (0)	17 (85)	0 (0)	0 (0)
			2175	2/3/03	80	12	0 (0)	475 (2833)	50 (333)	0 (0)
	we	Mount Elgon	2801	1/31/03	2389	1631	0 (0)	94 (138)	0 (0)	0 (0)
			2979	1/31/03	437	204	0 (0)	0 (0)	0 (0)	0 (0)
			2809	2/21/03	2000	1145	0 (0)	111 (194)	0 (0)	0 (0)

Table 2 (continued).

Plant species[2]	Region[3]	Location	Altitude (m)	Sampling date	No. of fruits	Weight (gms)	*B. biguttula* per 1000 fruit (per kg)	*B. oleae* per 1000 fruit (per kg)	*B. munroi* per 1000 fruit (per kg)	*M. whartoni* per 1000 fruit (per kg)
Olea europaea ssp *cuspidata*, green fruits	ce	Burguret Forest	1974	8/15/02	310	57	0 (0)	3 (18)	0 (0)	0 (0)
			1960	8/16/02	695	117	0 (0)	16 (94)	0 (0)	0 (0)
			2062	1/15/03	8570	940	0 (0)	1 (9)	0 (0)	0 (0)
Olea welwitschii	we	Kakamega Forest	1550	8/14/00	4219	1583	0 (0)	0 (0)	<1 (1)	0 (0)
			1550	8/15/00	267	145	0 (0)	0 (0)	4 (7)	0 (0)
			1550	9/12/00	445	184	0 (0)	0 (0)	7 (16)	0 (0)
			1630	9/19/00	98	40	0 (0)	0 (0)	0 (0)	0 (0)
			1550	9/20/00	1523	624	0 (0)	0 (0)	0 (0)	0 (0)
	we	Mau Forest	2332	8/2/01	28	35	0 (0)	0 (0)	0 (0)	0 (0)
Olea welwitschii, green fruits	we	Kakamega Forest	1550	6/2/00	638	206	0 (0)	0 (0)	0 (0)	0 (0)
	ce	Mount Kenya Forest	2448	4/9/02	69	104	0 (0)	0 (0)	0 (0)	0 (0)
Olea woodiana ssp *disjuncta*	co	Kaya Kinondo	5	7/20/00	161	38	0 (0)	0 (0)	0 (0)	0 (0)
	co	Shimba Hills	201	8/26/00	597	387	8 (13)	0 (0)	0 (0)	0 (0)

1. One *C. capitata* was reared from *O. europaea* ssp. *cuspidata* (2/23/2000) and 5 were reared from *O. woodiana* ssp. *disjuncta* (8/26/2000).

2. Ripe fruits sampled in all collections, except where indicated, when mature-sized, unripe green fruits were sampled.

3. ce = central highland forest, co = coastal lowland forest, we = western highland forest.

4. nd = tephritid positive sample, fruits neither counted nor weighed.

Table 3. Opiine parasitoids reared from tephritid-infested Oleaceae.

Plant species[1]	Region[2]	Location	Altitude (m)	Sampling date	No. fruits	Weight (gm)	no. of tephritids reared	Tephritid species	% of tephritids parasitized	Opiine wasps reared
Chionanthus niloticus	we	Koru; Brooks' farm	1565	6/4/00	1035	905	49	*M. whartoni*	2.0	*Psyttalia* sp., 1f
			1565	7/15/00	515	210	83	*M. whartoni*	0.0	
			1565	8/17/00	408	210	175	*M. whartoni*	4.9	*Psyttalia* sp., 7f, 2m
Olea europaea ssp. *cuspidata*	ce	Ololua Forest	1706	2/3/00	539	110	10	*B. oleae*	9.1	*Psyttalia* sp., 1m
			1823	2/23/00	nd[3]	nd[3]	4	*B. oleae*	0.0	
			1750	2/23/00	nd[3]	nd[3]	3	2 *B. oleae*, 1 *C. capitata*	0.0	
			1823	3/26/00	775	169	256	*B. oleae*	1.9	*Psyttalia* sp. cf *concolor,* 1f, 1m *Utetes africanus*, 1f, 1m *Psyttalia lounsburyi*, 1f
			1823	4/8/00	191	40	16	*B. oleae*	11.1	*Psyttalia concolor*, 1f *Utetes* sp[4], 1?
			1823	4/8/00	363	76	57	*B. oleae*	8.1	*Psyttalia concolor*, 1f, 4m
			1823	4/21/00	203	42	22	*B. oleae*	4.3	*Psyttalia lounsburyi*, 1m
			1823	4/28/00	nd[3]	nd[3]	3	*B. oleae*	25.0	*Psyttalia concolor*, 1f
	ce	Burguret Forest	1961	5/17/02	661	134	0			
			1974	8/15/02	2942	691	249	*B. oleae*	30.8	*Psyttalia lounsburyi*, 45f, 54m *Utetes africanus*, 8f, 4m
			1960	8/16/02	2235	535	388	*B. oleae*	19.8	*Psyttalia lounsburyi*, 34f,55m *Utetes africanus*, 5f, 2m
			2062	9/21/02	5000	1106	374	*B. oleae*	18.1	*Psyttalia lounsburyi*, 58f,24m *Utetes africanus*, 1f
			2010	11/13/02	1000	220	10	4 *B. oleae*, 6 *B. munroi*		

Table 3 (continued).

Plant species[1]	Region[2]	Location	Altitude (m)	Sampling date	No. fruits	Weight (gm)	no. of tephritids reared	Tephritid species	% of tephritids parasitized	Opiine wasps reared
Olea europaea ssp. *cuspidata*	we	Mau Forest	2187	9/19/00	235	47	4	*B. oleae*	20.0	*Psyttalia lounsburyi*, 1f
			2175	2/3/03	80	12	38	34 *B. oleae*, 4 *B. munroi*		
	we	Mt. Elgon	2809	1/31/03	2389	1631	225	*B. oleae*	0.4	*Psyttalia lounsburyi*, 1m
			2979	1/31/03	437	204	0			
			2809	2/21/03	2000	1145	222	*B. oleae*	0.9	*Psyttalia lounsburyi*, 2m
Olea europaea ssp. *cuspidata*, green fruits	ce	Burguret Forest	1974	8/15/02	310	57	1	*B. oleae*	0.0	
			1960	8/16/02	695	117	11	*B. oleae*	38.9	*Psyttalia lounsburyi*, 4f, 1m *Utetes africanus*, 1f, 1m
			2062	1/15/03	8570	940	8	*B. oleae*	50.0	*Psyttalia lounsburyi*, 3f,2m *Utetes africanus*, 2f, 1m
Olea welwitschii	we	Kakamega Forest	1550	8/14/00	4219	1583	1	*B. munroi*	0.0	
			1630	8/15/00	267	145	1	*B. munroi*	0.0	
			1550	9/12/00	445	184	3	*B. munroi*	0.0	
			1630	9/19/00	98	40	0			
			1550	9/20/00	1523	624	0			
	we	Mau Forest	2322	8/2/01	28	35	0			
Olea welwitschii, green fruits	we	Kakamega Forest	1550	6/2/00	638	206	0		0.0	
	ce	Mt. Kenya Forest	2448	4/9/02	69	104	0			
Olea woodiana ssp. *disjuncta*	co	Kaya Kinondo	5	7/20/00	161	38	0			
	co	Shimba Hills	201	8/26/00	597	387	10	5 *B. biguttula*, 5 *C. capitata*	0.0	

1. Ripe fruits sampled in all collections, except where indicated, when mature-sized, unripe green fruits were sampled.
2. ce = central highland forest, co = coastal lowland forest, we = western highland forest.
3. nd = tephritid-positive sample, fruits neither counted nor weighed.
4. Abdomen lost, probably *U. africanus*.

Table 4. Lepidoptera and non-opiine parasitoids reared from oleaceous fruits.

Plant species	% collns producing moths (total collns)	Species of moths reared	Total no. moths	Moths per kg[1]	Non-opiine Hymenoptera (excluding Chalcidoidea)	No. of wasps reared	Percent parasitization of moths
Chionanthus niloticus	67 (3)	Noctuidae: *Nola melanoscelis*	9	6.8	Braconidae: Braconinae sp. # 22	2	15.3
					Ichneumonidae: Cremastinae: *Pristomerus* sp	1	7.7
					Ichneumonidae: Banchinae	1	7.7
Jasminum dichotomum	0 (3)	none	0	0	Braconidae: Braconinae	1	100
Jasminum fluminense	40 (5)	Crambidae: Spilomelinae: *Palpita unionalis* Hübner	1	4.2		0	0
		Crambidae: Cybalomiinae: . *Hendecasis* sp. nr *duplifascialis* Hampson	3	12.6		0	0
		Microlepidoptera	1	4.2		0	0
Jasminum meyeri-johannis	67 (3)	Crambidae: Cybalomiinae: *Hendecasis duplifascialis*	1	1.6		0	0
		Microlepidoptera	3	4.8		0	0
Jasminum sp	33 (3)	Crambidae: Cybalomiinae: *Hendecasis duplifascialis*	1	5		0	0

Table 4 (continued).

Plant species	% collns producing moths (total collns)	Species of moths reared	Total no. moths	Moths per kg[1]	Non-opiine Hymenoptera (excluding Chalcidoidea)	No. of wasps reared	Percent parasitization of moths
Jasminum stenolobum	0 (3)	none	0	0	Braconidae: Cheloninae: Phanerotomini: *Phanerotoma* sp	1	100
Olea capensis ssp *macrocarpa*	0 (1)	none	0	0			
Olea europaea ssp *cuspidata*	19 (21)	Tortricidae	1	<1		?[2]	?
		Microlepidoptera	7	<1			
		Carposinidae	2	<1			
Olea welwitschii	38 (8)	Crambidae: Spilomelinae: *Dolicharthria lanceolalis*	1	0.3	Ichneumonidae: Cremastinae: *Pristomerus* sp.	2	22.2
		Microlepidoptera	6	2.1			
Olea woodiana ssp *disjuncta*	50 (2)	Microlepidoptera	1	2.3	Ichneumonidae: Cremastinae: *Pristomerus* sp.	1	50
Schrebera alata	50 (2)	Microlepidoptera	2	6.3			0

1. See Table 1 for total collection weight of each fruit species; includes moth-negative and -positive samples.
2. *Bracon* sp. were reared from fruits but because tephritids were present, cannot be confidently associated with a moth host

Munromyia whartoni Copeland, **sp**. **nov**., a new species of the previously monotypic adramine genus *Munromyia* Bezzi, was reared from *Chionanthus niloticus* fruits collected in gallery forest in western Kenya (Table 2). A description of this species and a key to the *Munromyia* are provided below. The fruiting season of *C. niloticus* was sharply defined, beginning at the end of the "long" rainy season and lasting 3 months. *Munromyia whartoni* was reared from each of three monthly collections of fruit made over this period. Population density of *M. whartoni*, as measured by the infestation index, increased steadily over the fruiting period in 2000, after which fruits were not found (Table 2). Fruiting of its host, *C. niloticus*, was not seen during repeated visits to the same site in 2001 and 2002.

Four tephritids were reared from *Olea*: the medfly, *Ceratitis capitata* (Wiedemann), and 3 species of *Bactrocera* Macquart. The medfly was recovered, infrequently and in small numbers, from collections of *O. woodiana* ssp. *disjuncta* at the coast and *O. europaea* ssp. *cuspidata* in the central highlands as previously reported (Copeland *et al*., 2002). *Bactrocera oleae* was reared exclusively from *O. europaea* ssp. *cuspidata* in highland forests both east (1706–2062 m) and west (2175–2809 m) of the Gregory Rift Valley. *Bactrocera biguttula* (Bezzi) was found only in fruits of *O. woodiana* ssp. *disjuncta*, in lowland forest (201 m) near the Kenyan coast. A previously unknown species of *Bactrocera, Bactrocera munroi* White, **sp**. **nov**., was reared in relatively small numbers from both *O. europaea* ssp. *cuspidata* (central and western highland collections, 1970–2175 m) and from *Olea welwitschii* (Knobl.) Gilg & Schellenb. from Kakamega Forest (1550 m), the easternmost extension of Guineo-Congolian equatorial forest. Descriptions of the new species and a key to the African subgenera of *Bactrocera* are found below.

The olive fly was reared from 16 of 18 collections of ripe fruits of *O. europaea* ssp. *cuspidata*, and from all 3 collections of green fruits. From matched collections of ripe and green fruits at 2 separate locations in Burguret Forest, ripe fruits produced significantly more *B. oleae* per fruit than did green fruits (site 1 [1974 m], $X^2 = 25.06$, d.f. = 1, p = <0.0001; site 2 [1960 m], $X^2 = 110.85$, d.f. = 1, p = <0.0001). Two collections of ripe fruits of *O. europaea* ssp. *cuspidata*, made on Mt. Elgon at 2801 and 2809 m, represented the highest altitude at which *B. oleae* was reared from olives (Table 2). The only sample of olives taken at a higher elevation (2979 m, also on Mt. Elgon) failed to produce *B. oleae*.

Tephritid parasitoids were reared from *M. whartoni* and *B. oleae* (Table 3). A single, possibly undescribed species of *Psyttalia* Walker (Hymenoptera, Braconidae, Opiinae) was reared from 2 of 3 fruit samples that produced *M. whartoni*. Parasitization rates were relatively low, approaching 5% during the final month's collection. Three species of Opiinae were recovered from *B. oleae*: *Psyttalia lounsburyi* (Silvestri), *P. concolor*, and *Utetes africanus* (Szépligeti). A few individuals of *Bracon celer* (Szépligeti), of the braconid subfamily Braconinae, were also reared. In our collections, *P. lounsburyi* was both more common and widespread than *U. africanus* and *P. concolor*. The latter was found only in collections from Ololua Forest in Central Kenya. No wasps were recovered from samples of fruits that produced *B. munroi*, *B. biguttula*, or *C. capitata*, however few individuals of these latter 3 species were reared.

Lepidoptera and their parasitoids

Moths were reared from all four genera of Oleaceae, and were the only frugivores that attacked *Schrebera* and *Jasminum* species (Table 4). *Jasminum* fruits were preyed upon by 3 species of Crambidae, representing 2 crambid subfamilies. A *Hendecasis* sp. nr. *duplifascialis* Hampson was the only species that attacked more than one host.

Species richness of frugivorous moths was highest in *O. europaea* ssp. *cuspidata*, from which a tortricid, a carposinid, and an unplaced microlepidopteran were reared. Single moth species were reared from *S. alata*, *O. welwitschii*, and *C. niloticus*.

Relatively few parasitoids of Lepidoptera were found in our samples. These comprised two genera each of Ichneumonidae and Braconidae (Table 4).

Chalcidoidea

Most of the chalcidoid wasps we reared represent genera that contain both phytophagous species as well as parasitoids. Since our rearing protocol did not allow us to determine the trophic status of chalcidoid species, we consider them here as one group. Chalcidoids were reared from 33% (n = 21) of *O. europaea* ssp. *cuspidata* collections. Most of these were Eurytomidae, including undetermined species of both *Eurytoma* Illiger and *Sycophila* Walker. Also reared were a pteromaline Pteromalidae, a tetrastichine Eulophidae, and undetermined species of *Pseudotorymus* Masi (Torymidae) and *Eupelmus* Dalman (Eupelmidae). The only other fruit species from which chalcidoids were reared was *O. welwitschii* from which 2 undetermined species, one a eulophid and the other a eupelmid, were reared.

Taxonomy of the genus *Munromyia* Bezzi

Munromyia is placed in the subfamily Trypetinae, tribe Adramini. The limits of the Adramini (Trypetinae) have been difficult to define, leading to widely different interpretations of which genera belong in it [e.g., Hancock (1986), 3 genera including *Munromyia*; Hardy (1986), 20 genera]. Recent studies have greatly increased the number of adramine genera, largely because of the absorption into it of most of the genera previously assigned to the Euphrantini (Norrbom *et al.*, 1999a; Korneyev, 1999). Currently, 181 species in 26 genera are recognized. Primarily composed of Australasian and Oriental species, the tribe is represented in the Afrotropical region by 32 species in 8 genera (Norrbom *et al.*, 1999a,b).

Bezzi (1922) described *Munromyia* from specimens of *Munromyia nudiseta* Bezzi reared by Munro (1924) from fruits of *Chionanthus foveolatus* (E. Mey.) Stearn (as *Olea foveolata* E. Mey.). Bezzi (1922) recognized the similarity of the new genus to both *Meracanthomyia* Hendel and to *Adrama determinata* (Walk.) and, accordingly, erected the monospecific genus *Munromyia* and placed it in the Adramini (as Adraminae), where it still resides.

Key to species of *Munromyia* Bezzi

1. Median stripe of scutum black, narrow, separated from whitish dorsocentral lines by a distance about equal to width of median stripe (Fig. 4a), solid, not bisected. Scutellum uniform in color, reddish orange (Fig. 4a). Abdominal syntergite 1+2 entirely black (Figs. 4a & 4c). Anepisternum uniform in color, reddish-orange (Fig. 4c). Basal margin of apical wing spot forming an acute angle with costa, spot dark, mostly gray-brown (Fig. 5a). Aculeus ca. 8.3 × as long as wide (width measured at apex of 8th sternite [Fig. 5d]). Distiphallus with 2 rows of strongly curved, boomerang-shaped cuticular processes with finely tapered, untoothed tips (Fig. 6a) ……………………………............….….. ***Munromyia whartoni*** Copeland, **sp. nov.**

–. Median stripe of scutum black or blackish-red, wide, filling nearly entire area between whitish dorsocentral lines, median stripe bisected by thin black line bordered by equally thin whitish lines (Fig. 4b). Scutellum bicolored, base and disk very dark red-brown, apex yellow-white (Fig. 4b). Abdominal syntergite 1+2 orange medially with anterior, lateral, and posterior margins black (Figs. 4b, 4d). Anepisternum tricolored with black band separating anterior reddish-orange area from posterior yellow-white area (Fig. 4d). Basal margin of apical wing spot forming an obtuse angle with costa, spot light brown (Fig. 5b). Aculeus ca. 13.2 × as long as wide (width measured at apex of 8th sternite [Fig. 5e]). Distiphallus with two rows of weakly curved cuticular processes, one row with most processes having at least 1 tooth (Fig. 6b), the other row with all or most processes lacking teeth ……................................ ***Munromyia nudiseta*** Bezzi

Munromyia whartoni Copeland, **new species**

Material examined. – Holotype – male (NMKE), KENYA: Nyanza Province, Koru / Brooks' Farm, 0°07.70' S, 35°16.69' E, 15.vii.2000, ex fruit *Chionanthus niloticus*, ICIPE/USAID collection 757, leg. R.S. Copeland, MNSP5, USNM ENT 00214327. Paratypes - 37 males (2 dissected), 45 females (2 dissected), Nyanza Province, Koru / Brooks' Farm, 0°07.70' S, 35°16.69' E, 15.vii.2000, ex fruit *Chionanthus niloticus*, ICIPE/USAID collection 757, leg. R.S. Copeland; 30 males, 19 females, same data except ICIPE/USAID collection 707, 4.vi.2000; 80 males, 95 females, same data except ICIPE/USAID collection 810, 17.viii.2000.

Paratypes to be distributed between NMKE, BMNH, MRAC, USNM, SANC, Texas A&M University, USA, Tel Aviv University, Israel, and the International Centre of Insect Physiology and Ecology (ICIPE), Nairobi, Kenya.

Description. – Male (habitus, Fig. 8a). Body length 6.4–7.4 mm. Head – Scape and pedicel orange. First flagellomere black, except for short yellowish portion basad to arista; 10.4 × as long as wide, and 3 × combined length of scape and pedicel. Arista dark, except light basally; about equal in length to first flagellomere. Face orange, except for two large subantennal black spots. Frons orange, except for black ocellar triangle; 3, occasionally 2, pairs of frontal setae, dorsal pair 2 × as far from middle pair as ventral pair. Ocellar seta shorter than length of ocellar triangle. Orbital setae absent. Occiput orange, except for dark brown-black area behind middle of eye.

Thorax (Figs. 4a, 4c) - Length 2.6–2.9 mm. Ground color orange. Black medial stripe extending from posterior margin of scutum, nearly reaching anterior margin. A single pair of thinner, less distinct whitish dorsocentral stripes lateral to and parallel with black stripe, and separated from it by distance approximately equal to width of black stripe. Lateral scapular seta present, medial scapular absent. Anterior and posterior notopleural setae present. Presutural supra-alar seta absent. One pair each of postsutural supra-alar, postalar, and intra-alar setae. Intrapostalar seta absent. Anepisternum uniformly orange, one anepisternal seta. Katepisternum black, katepisternal seta absent. Anepimeral seta present. Scutellum uniformly orange. Basal and apical scutellar setae present.

Wing (Fig. 5a) – Length 5.1–5.8 mm, hyaline, with hemi-elliptic dark gray-brown apical spot covering about 1/3 of wing. Basal margin of spot forming slightly acute angle with costa. Spot covering, on average, 0.27 (0.25–0.30) combined length of veins Rs + R_{2+3}, 0.52 (0.49–0.54) length of R_{4+5}, and 0.74 (0.71–0.76) length of M. Pterostigma gray-brown, with narrow, irregularly-shaped, gray-brown band extending from its base to near intersection of bm-cu and CuA_1. Halter yellow.

Legs (Fig. 4c) - Yellow to yellow-orange. Fore femur with subapical brownish-black spots, covering apical 1/3 of anterior and posterior surfaces. Mid femur brown-black over apical 2/3. Hind femur brown-black over apical 1/2. Fore, mid, and hind tibiae brown to brown-black. Hind coxa brown-black. Fore femur with single row of ventral spines on apical 1/2. Mid and hind femora with two parallel rows of ventral spines on apical 1/2–2/3 and apical 1/2, respectively.

Abdomen (Figs. 4a, 4c) - Syntergite 1+2 black, tergites 3–4 orange or dark orange, tergite 5 orange.

Terminalia (Fig. 7) - Epandrium nearly spherical, lateral surstylus elongate, in lateral view tapering to blunt point, prensisetae globular. Distiphallus with 2 rows of boomerang-shaped cuticular processes, each tapered at apex to a fine point. Glans elongate, columnar.

Description. - Female. Similar to male, except tergites 3–6 and oviscape usually orange, sometimes dark orange. Body length 8.1–8.8 mm. Thorax length 2.8–3.0 mm. Wing length 5.7–6.0mm. Eversible membrane with 2 ventral and 3 dorsal taeniae. Ventral pair solidly sclerotized on basal 1/5–1/4 of eversible membrane, becoming rows of teeth increasing gradually in size until reaching ca. middle of eversible membrane, whereupon they diminish in size, becoming minute and covering rest of ventral surface including space between taeniae. Dorsal taeniae solidly sclerotized on basal 1/8–1/10 of eversible membrane, becoming rows of teeth increasing in size and then diminishing as for ventral taeniae, except dorsal taeniae also with ca. 8–12 pronouncedly larger clamshell-shaped teeth (Fig. 5c) spread along this length. Size of clamshell-shaped teeth greater in middle taenia. Spaces between lateral and middle taeniae without any teeth on ca. basal 1/5 of eversible membrane. Aculeus tapered, then slightly broadened at base of tip, ca. 1.2 mm long (Fig. 5d), ca. 8.3 × as long as wide (measured at apex of 8th sternite); tip broadly triangular, evenly tapered. Three spermathecae, more or less elongate and vase shaped, swollen apically, base slightly flared with serrate projections surrounding spermathecal duct. Surface densely covered with slender, acute denticles.

Host: - *Chionanthus niloticus* is the only known host of *M. whartoni*.

Remarks: - *Munromyia whartoni* is known only from a single gallery forest surrounded by subsistence farms and commercial sugar cane plantations in western Kenya. This species is most closely related to *M. nudiseta*, based on similarities in both physical and behavioral characteristics (see discussion). Nonetheless, it is readily distinguished from its congener by the coloration of the anepisternum and scutellum, by the relative width of the medial vitta of the scutum, and by the shape of the apical wing spot. Characters of both male and female genitalia are also useful in separating the species and show that they are not simply color morphs of the same species.

Etymology: - This species is named in honor of Bob Wharton whose scholarship and enthusiasm for field biology are an inspiration.

Taxonomy of *Bactrocera* subgenus *Daculus* Speiser

There are approximately 500 described species of *Bactrocera*, only 10 of which are native to Africa [see Norrbom *et al.* (1999b) for details of nomenclature and synonomy], the remainder being found in the Asian, Australasian and Pacific regions. In addition, 2 species of Asian origin are now established in Africa: *B.* (*B.*) *zonata* (Saunders) (in Egypt, Mauritius and Réunion) and *B.* (*Zeugodacus*) *cucurbitae* (Coquillett) (in East Africa, Mauritius, Réunion and West Africa). Conversely, 1 native African species, the olive fly, *B.* (*Daculus*) *oleae* (Rossi), is widespread in the Mediterranean area and has recently become established in California. A second African species of *Bactrocera* associated with *Olea europaea* is described here, together with a brief review of related African *Bactrocera* spp.

Most of the native African *Bactrocera* spp. have been placed in the subgenera *Afrodacus* Bezzi, *Daculus* Speiser and *Gymnodacus* Munro, all of which have African type species (*Chaetodacus biguttulus* Bezzi, *Musca oleae* Rossi and *Dacus mesomelas* Bezzi, respectively). The only exception is *B.* (*B.*) *nesiotes* Munro, whose true position cannot be ascertained as no male has been collected. These subgenera are characterized by differences in secondary sexual characters and chaetotaxy (see key for details), although the latter has been shown to be a poor basis for subgeneric classification (White, 1999).

Most taxonomic studies of *Bactrocera* spp. have been of a regional nature but the world species of *Afrodacus* and *Gymnodacus* were reviewed by Hardy (1955, 1954, respectively), who included some non-African species in those subgenera, as have subsequent authors. However, White & Evenhuis (1999) suggested that Asian species assigned to the subgenus *Gymnodacus* might be more closely allied to *Bulladacus* Drew & Hancock, than to true African *Gymnodacus*. Similarly, non-African species hitherto assigned to the subgenus *Afrodacus* should be regarded as species of the subgenus *Bactrocera* with atypical chaetotaxy. The difference between *Afrodacus* spp. and *Daculus* is small (presence or absence of prescutellar acrostichal setae) and, since both groups include olive associated species with shared morphological features (see key), *Afrodacus* is here placed in synonymy with *Daculus*. The larvae of 3 species, *B.* (*D.*) *oleae*, *B.* (*D.*) *biguttula* (Bezzi), and *B.* (*D.*) *munroi,* or perhaps their common ancestor, adapted to the oily and presumably hostile environment of the olive fruit.

The following nomenclatural changes are made:
The subgenus *Afrodacus* Bezzi 1924: 469, type species *Chaetodacus biguttulus* Bezzi, by monotypy [published August 1924, Carroll *et al.* (1998)] is a new synonym of subgenus *Daculus* Speiser 1924: 140, type species *Musca oleae* Rossi, by original designation [published 18th July 1924, Carroll *et al.* (1998)].

The following non-African species, previously placed in the subg. *Afrodacus*, are now placed in the subg. *Bactrocera* s.str.: *B. brunnea* (Perkins & May), *B. fastigata* Tsuruta & White, *B. grandistylus* Drew & Hancock, *B. hypomelaina* Drew, *B. jarvisi* (Tryon), *B. minuta* (Drew), *B. ochracea* Drew. The African species newly transferred to the subg. *Daculus* are listed in the following key.

Annotated key to African *Bactrocera* subgenera and subgenus *Daculus* species

1. Yellow or orange mark extended across both anatergite and katatergite (covers the centers of both sclerites). [Scutum with anterior supra-alar and prescutellar acrostichal setae. Male with a pecten] .... subg. ***Bactrocera*** Macquart

–. Yellow mark, if present, confined to katatergite, or at most slightly extended onto anatergite ... 2

2. Scutum with anterior supra-alar setae. Male without a pecten (or pecten reduced to a few fine hairs). Male costa between costagial break and humeral crossvein with stout setulae (stouter than on section before costagial break) .... subg. ***Gymnodacus*** Munro

–. Scutum without anterior supra-alar setae. Male with a pecten. Male costa between costagial break and humeral crossvein without stout setulae (setae similar before and after costagial break) .... subg. ***Daculus*** Munro ... 3

3. Wing with a narrow dark marking along crossvein r-m (sometimes indistinct). Scutellum concolorous with scutum. Scutum without lateral postsutural vittae 4

–. Wing without any markings along crossveins. Scutellum not concolourous with scutum (yellow, with either a narrow basal darker line, dark apically, or largely dark and laterally yellow). Scutum usually with lateral postsutural vittae (absent in *B. oleae*; sometimes hard to discern or faded in other species) 5

4. Face with a dark spot in antennal furrow. Notopleural callus yellow. Microtrichia throughout the narrow section of cell br. [South Africa; host unknown] .... ***lucida*** (Munro)

–. Face without a dark spot in antennal furrow. Notopleural callus concolorous with scutum. Microtrichia confined to anterior edge of narrow section of cell br. [Kenya, South Africa; host is *Duranta erecta* L. (Verbenaceae; Munro, 1984 (as *Duranta repens*), R. Copeland, unpubl. data)] .... ***nigrivenata*** (Munro)

5. Wing with a very large apical dark marking that extends from anterior (costal) edge to at least vein M 6

–. Wing with costal band at most slightly enlarged apically 7

6. Scutum black. Scutellum markings black; either largely black, yellow laterally; or with a conspicuous black apical spot. [Mauritius and Réunion. Known host *Calophyllum tacamahaca* Wildd. (Clusiaceae; S. Quilici *pers. comm.*)] .... ***montyanus*** (Munro)

-. Scutum red-brown. Scutellum yellow, except for narrow red-brown basal margin and trace of red-brown apical spot. [Madagascar; host unknown.] .... ***menanus*** (Munro)

NOTE: *Dacus andriae* Munro was recently placed in synonymy with *B. menanus* by Hancock & Drew (2001).

7. Scutum without prescutellar acrostichal setae. Scutellum with dark colored (fuscous to black) basal band or triangle; yellow laterally and apically .... ***oleae*** (Rossi)

-. Scutum with prescutellar acrostichal setae. Scutellum with a colored (red brown to black) marking from base to apex; yellow laterally 8

NOTES: *Bactrocera* (*Daculus*) *oleae* is found in eastern and southern Africa (Eritrea, Kenya, Lesotho, South Africa), and throughout the olive growing areas of the southern Palaearctic (including North Africa); it has recently become established in California, USA. In Kenya its host is *O. europaea* ssp. *cuspidata* (RSC data from Central and Western Highlands); in South Africa *O. europaea* ssp. *cuspidata* (Munro, 1924, as *O. verrucosa*) and cultivated olive, *O. europaea* ssp. *europaea* (Hancock, 1989).

8. Scutum red-brown with a pair of black or dark submedial stripes, which may be divided or partly divided at suture, and which broaden apically. Abdomen red-brown, with a pair of dark sublateral or lateral markings on tergite III and sometimes tergite IV. Face with a medium sized (0.16–0.24mm in South Africa, 0.20–0.25mm wide in Kenya) dark spot in each antennal furrow .... ***biguttula*** (Bezzi)

-. Scutum predominantly black; sometimes fuscous medially (paler if teneral). Abdomen predominantly black; usually fulvous across apex of tergite II and sometimes with paired red-brown areas sub-medially on tergite IV, and sometimes III. Face usually with small to very small dark spots (up to 0.12mm wide in Kenya, 0.16mm wide in Ruwenzori area); sometimes completely lacking .... ***munroi*** White, **sp. nov**.

NOTES: *Bactrocera* (*Daculus*) *biguttula* is known from Kenya (Coast Province), Mozambique and South Africa. In Kenya its only known host is *O. woodiana* ssp. *disjuncta* (RSC data); in South Africa it is recorded from *Olea capensis* ssp. *capensis* (Munro, 1924, as *O. laurifolia*), *O. woodiana* and *Chionanthus foveolatus* (Munro, 1924, as *O. foveolata*).

Specimens examined of *B. biguttula* – KENYA: 1 male (dissected, BMNH), 4 females (1 dissected, BMNH), Coast Province, Shimba Hills, 26.viii.2000, reared ex *O. woodiana* ssp. *disjuncta*, leg. R.S. Copeland, sample 824/K702. SOUTH AFRICA: 1 male, 2 female, paralectotypes, East London, 4–10.vii.1922, leg. H.K. Munro, reared ex *O. woodiana* (MSNM); 9 males,

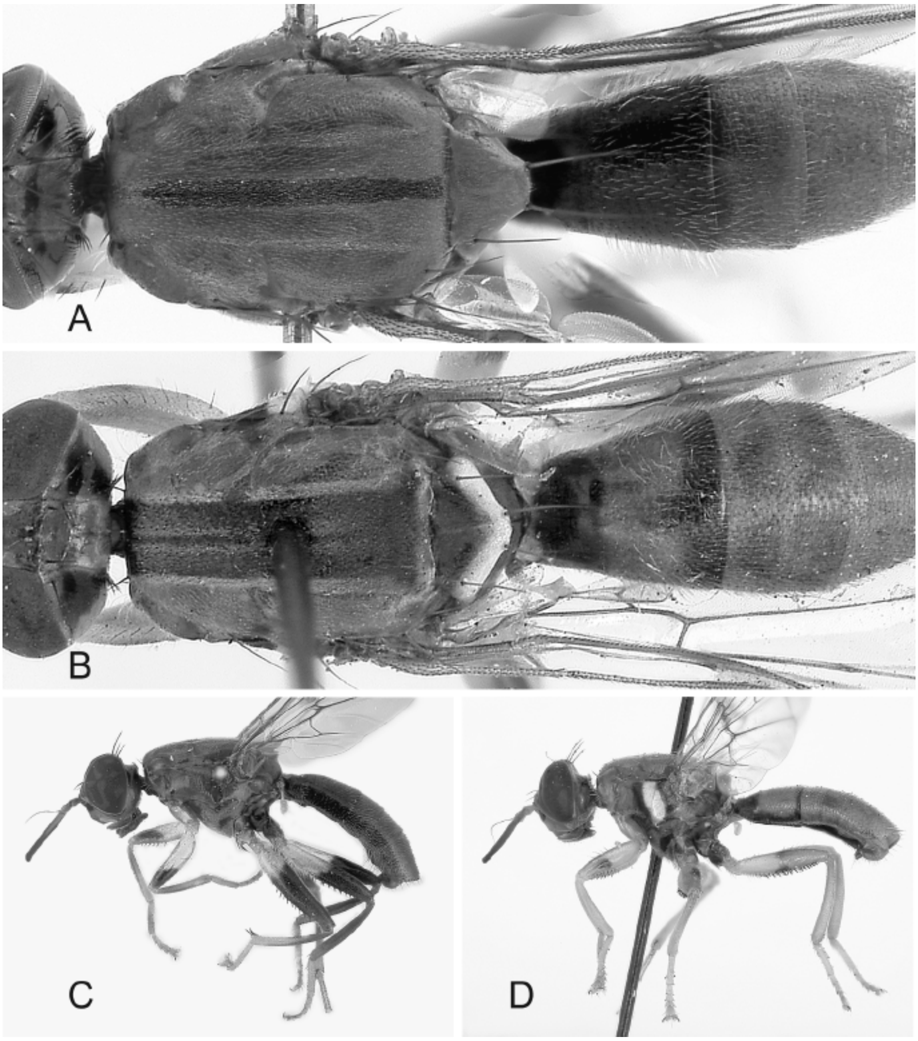

Figure 4. Habitus figures. **a**. *M. whartoni*, dorsal; **b**. *M. nudiseta*, dorsal; **c**. *M. whartoni*, lateral; **d**. *M. nudiseta*, lateral.

11 females (SANC), various localities, including specimens reared from all listed hosts (SANC). MOZAMBIQUE: 1 male, 1 female (SANC), Lourenço Marques, 10.v.1937, leg. J. Lima, not reared.

Bactrocera (Daculus) munroi White, **new species**

Dacus (Afrodacus) biguttulus: Munro 1957: 860, not Bezzi 1922: 294, misidentification.

Material examined. – Holotype male (NMKE), KENYA: Western Highlands, Rift Valley Province, Mau Forest (0°14.13' S, 35°32.94' E), 2175 m, 3.ii.2003, reared ex fruit *Olea europaea* ssp. *cuspidata*, sample A&M 2460, leg. R.S. Copeland. Paratypes - 2 males (1 dissected), 1 female, same data as holotype. KENYA: 1 male, 2 females (1 dissected), Central Highlands, Central Province, Burguret Forest (0°6.87' S, 37°3.29' E), 13.xi.2002, reared ex fruit *Olea europaea* ssp. *cuspidata*, sample A&M 2301, leg. R.S. Copeland; 1 female, Western Highlands, Western Province, Kakamega Forest (0°14.13' N, 34°51.87' E), 1550m, 14.viii.2000, reared ex fruit *Olea welwitschii*, sample A&M 821, leg. R.S. Copeland; 1 male, 2 females, same locality, 12.ix.2000, reared ex fruit *Olea welwitschii*, sample A&M 884, leg. R.S. Copeland; 1 female (dissected), same locality, 29.iii.2000, reared ex fruit *Prunus africana*, sample A&M 574, leg. R.S. Copeland; 3 males (1 dissected), 1 female, same locality (0°13.14' N, 34°54.14' E), 1630m, 13.iv.1999, reared ex fruit *Prunus africana*, sample A&M 67, leg. R.S. Copeland; Kenyan paratypes to be distributed between BMNH, MRAC, NMKE and SANC. DEMOCRATIC REPUBLIC OF CONGO: 1 female (MRAC), Kivu, Rwankivi, 3.xii.1943, leg. J.V. Leroy. UGANDA: 1 female (BMNH), Katwe, 26.xii.1934, leg. F.W. Edwards.

Description. – male. Head - Pedicel + 1st flagellomere not longer than ptilinal suture. Face usually with dark spot in each antennal furrow (sometimes absent in males, rarely absent in females; if present, usually small (about 0.10mm wide), rarely larger (0.16mm in Congo and Uganda specimens) and round. No other facial markings. Frons with 2 pairs of frontal setae; without spots at seta bases.

Thorax - Predominant color of scutum black, sometimes fuscous or narrowly dark red-brown medially. Postpronotal lobe partly pale, dark anteromedially. Notopleural lobe yellow. Notopleural suture without isolated wedge shaped mark. Scutum with lateral postsutural vitta (yellow; narrow; sometimes tapered; not extended anterior to suture; extending posteriorly almost to posterior supra-alar seta; sometimes indistinct). Scutum without medial vitta. Scutellum patterned; black or dark fuscous from base to apex, yellow laterally. Anepisternum with yellow band from notopleuron to (or almost to) katepisternum; narrow, dorsally not reaching anterior notopleural seta. Katepisternal mark about as broad as anepisternal stripe (at katepisternum-anepisternum suture). Yellow marking on hypopleural callus confined to katatergite. Notopleuron with anterior seta. Scutum without anterior supra-alar or prescutellar acrostichal seta. Scutellum without basal setae.

Wing – Length, 4.3–5.1mm. Cells bc and c with microtrichia confined to anteroapical corner. Cell br (narrowed part) with microtrichia confined to anterior half. Cell bm without microtrichia. Crossvein R-M distal to middle of cell dm. Costal band shallow (or incomplete), not extending posterior to R_{2+3}, slightly expanded apically. Wing with anal streak. Cells bc and c hyaline. No other wing patterning.

Legs – All femora, fore and mid tibiae yellow; hind tibia fulvous.

Abdomen - Predominant colour of abdomen red-brown to black. Tergites not fused. Abdomen not petiolate. Tergites III and IV entirely dark, or red-brown submedially (leaving medial dark stripe).

Terminalia and secondary sexual characters - Tergite III with pecten (setal comb) on each side. Basal costal sections without thicker setulae than other sections. Wing with deep indent in posterior margin; with microtrichia around apex of vein A_1+CuA_2. Hind tibia with preapical pad. Surstylus apex evenly rounded to point (apparently identical to that of *B. biguttula*; figured by Munro, 1984, Fig. 19).

Description. – female (habitus, Fig. 8b) – Aculeus length 1.0mm (2 measured; indistinguishable from *B. biguttula* in shape or length); apex pointed. Other characters as male except secondary sexual characters (i.e. tergite III without pecten; wing without deep indent in posterior margin; without microtrichia area around apex of vein A_1+CuA_2; hind tibia without preapical pad).

Hosts. – All of the Kenyan specimens were reared, mostly from wild olives, namely *O. europaea* ssp. *cuspidata* and *O. welwitschii.* However, this species was also reared from *Prunus africana* (Hook.f.) Kalkm. on two separate occasions, indicating that this is probably a normal host association. All 3 plant hosts are distributed in mid or high altitude, inland forests. This contrasts to the hosts of *B. biguttula* (listed above), all of which have predominantly lowland, coastal distributions both in Kenya (Beentje, 1994) and southern Africa (Cotes Palgrave, 1983). *Bactrocera biguttula* has never been recorded from *Olea europaea*, and aside from the rather odd association with *Prunus*, *B. munroi* has more in common in its host relationships with *B. oleae* than it does with *B. biguttula*. *Bactrocera munroi* and *B. oleae* were reared from the same sample of *O. europaea* ssp. *cuspidata* from Burguret Forest, Central Highlands, Kenya (R. Copeland, unpubl. data).

Remarks. – *Bactrocera munroi* is known only from highland areas close to the equator, from the Ruwenzori area of eastern Congo and Uganda, to the highland areas of Kenya, west (Kakamega

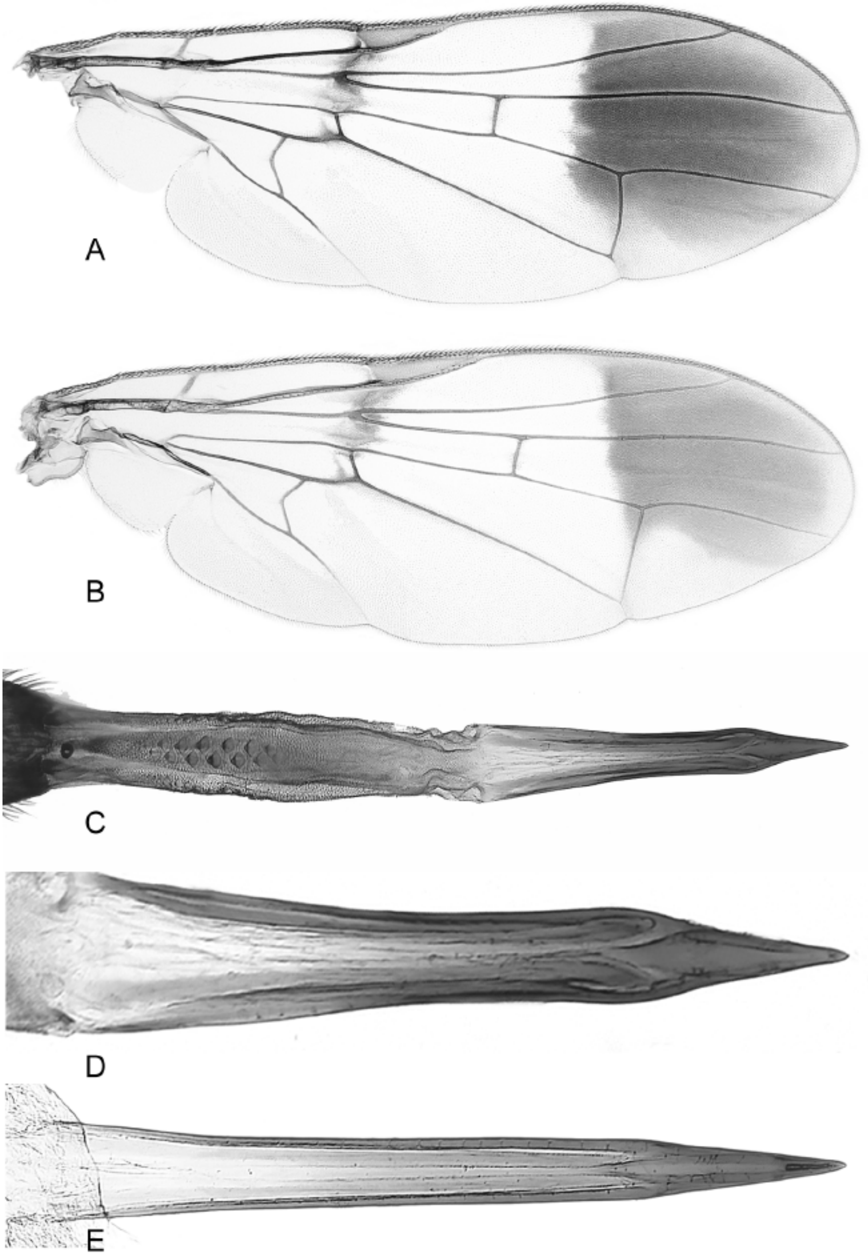

Figure 5. **a**. *M. whartoni*, wing; **b**. *M. nudiseta*, wing; **c**. *M. whartoni*, eversible membrane and aculeus; **d**. *M. whartoni*, aculeus; **e**. *M. nudiseta*, aculeus.

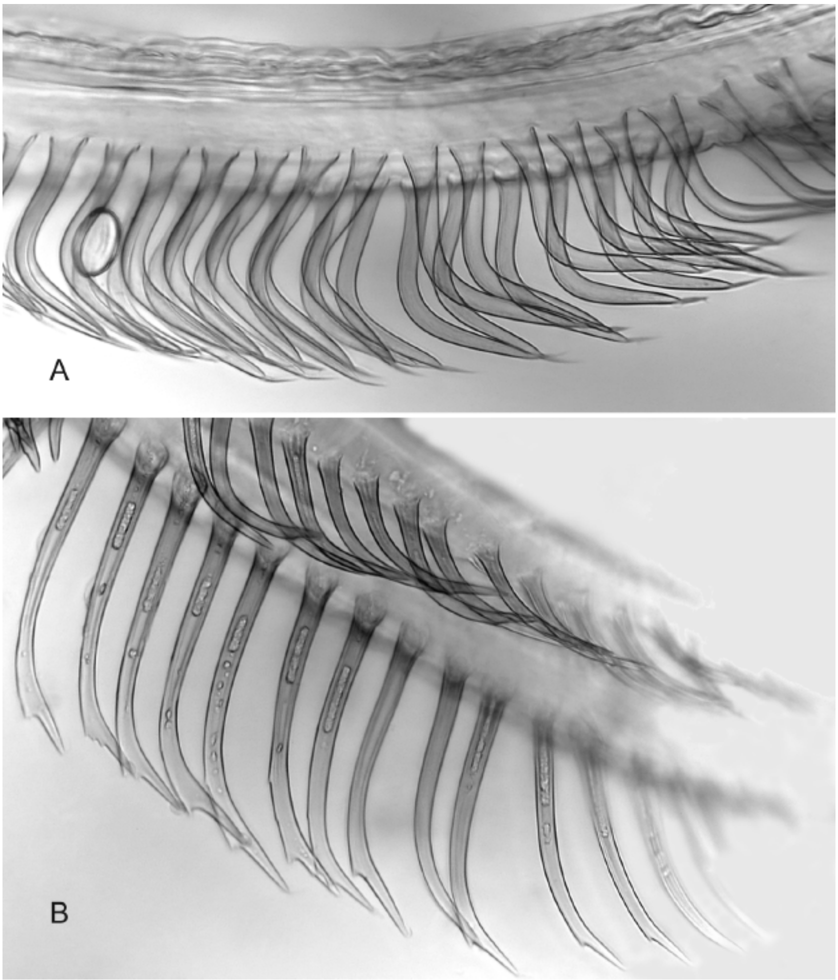

Figure 6. **a**. *M. whartoni*, cuticular processes on distiphallus, **b**. *M. nudiseta*, cuticular processes on distiphallus.

Forest and Mau Forest) and east (Burguret Forest, Mt. Kenya) of the Rift Valley. It is a much darker fly than *B. biguttula* and usually has smaller facial spots, or no facial spots at all, although no other differences have been detected (the aculeus, surstyli and glans of Kenyan specimens of both species appear to be nearly identical). The facial spots of *B. munroi* are variable. In Kenyan specimens the spots are either very small or absent whereas in the two specimens known from the Ruwenzori they are larger (0.16mm), but still smaller than most *B. biguttula* (0.16-0.25mm). Specimens from both *O. welwitschii* and *O. europaea* ssp. *cuspidata* either lack facial spots or have small facial spots (0.10-0.12mm wide); presence and absence has been observed in both sexes and from both hosts; specimens from *P. africana* all have small spots (c. 0.10mm). The Ugandan specimen is paler than the other specimens, with the scutal stripes slightly more similar to the pattern seen in typical *B. biguttula*. It also has what appears to be an irregular shaped narrow medial postsutural vitta, but it is a damaged and rather teneral specimen, and its pale scutum pattern and apparent vitta may be no more than artifact.

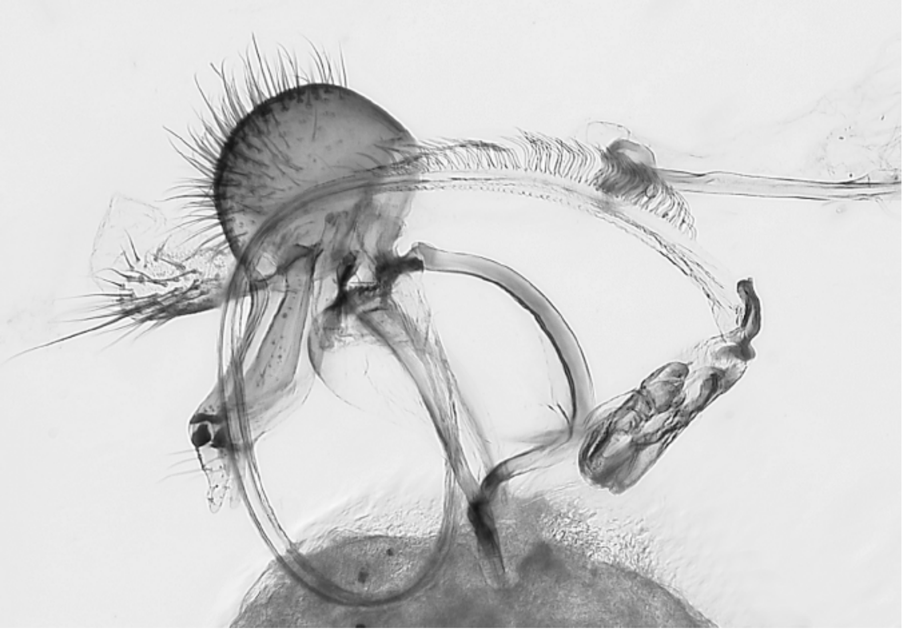

Figure 7. *M. whartoni*, male terminalia.

Etymology. – This species is named after H.K. Munro, in honour of his 60 years of research on African Tephritidae, which began in 1924 with his study of the fruit flies of wild olives.

Discussion

Munromyia whartoni is known from a single gallery forest on one farm in western Kenya. Similar small patches of forest are found throughout the agricultural areas of southern Kenya. As a whole, these forest relicts may harbor significant numbers of undescribed and threatened species. It is not known how local populations of *M. whartoni* or, for that matter, *B. oleae* survive over long periods in the apparent absence of their only known hosts, but some previous observations may be relevant. Munro (1924) was able to keep adults of *M. nudiseta* alive in the laboratory for 11 months, and adults of Mediterranean populations of *B. oleae* are known to enter a facultative reproductive diapause during hot summer months or months when fruits are absent (Fletcher, 1989). Nothing is known about the behavior or longevity of Kenyan *B. oleae* or *M. whartoni*, but it is possible that physiological adaptations play a role in maintaining populations of these species. Additionally, although fruiting of *C. niloticus* and *O. europaea* ssp. *cuspidata* (in Ololua Forest) was uniform and intense during only one year of our sampling, small numbers of fruit may appear on few trees (as they did in Ololua Forest) during "non-fruiting" years, providing enough nutritional substrate to support a breeding population of flies.

Like *M. nudiseta, M. whartoni* larvae attack the seeds of *Chionanthus* fruits. Pupation took place exclusively within the fruit (R. Copeland, pers. observ.) a behavior also noted by Munro (1924). The adults of both species are apparent mimics of aculeate Hymenoptera (Fig. 8a), exhibiting rapid wasp-like movements of both the wings and the abdomen (Munro 1924; R. Copeland, pers. observ.). Both

Munromyia species also have interesting structures on the male and female genitalia. In addition to the denticles often found on the eversible membrane of tephritid females, there is a small series of larger clamshell-shaped projections. What may be homologous structures occur on the eversible membrane of *Adrama magister* Lee (Lee, 1991). In addition, males of both species possess 2 rows of pronounced cuticular processes projecting out from the surface of the distiphallus. Apparently similar structures are found on the distiphallus of some males of the otitid subfamily Otitinae (Steyskal, 1987; p. 803) and of the tephritine fruit fly *Freidbergia mirabilis* Merz (Merz, 1999; p. 657). The functions of these structures of the male and female terminalia of *Munromyia* are unknown.

Previously, *Munromyia* was known only from the type species, whose distribution is limited to Eastern Cape Province, South Africa. The discovery of a second species in western Kenya increases the range of *Munromyia* by ca. 3600 km, across 30 degrees of latitude. Two other *Chionanthus* species are found in Kenya. *Chionanthus battiscombei* (Hutch.) Stearn is widely distributed in dry forests above 850 m, and *Chionanthus mildbraedii* (Gilg. & Schellenb.) Stearn is known from wet forests above 1550 m in the western part of the country. We were unable to find fruiting specimens of either species and it would be of interest to discover whether *Munromyia* breed in seeds of their fruit.

Unlike South Africa, where *B. oleae* also breeds in introduced commercial olive (*O. europaea* ssp. *europaea*) (Hancock, 1989), in Kenya, the indigenous olive *O. europaea* ssp. *cuspidata* is the only known host. Although commercial olive was introduced into Kenya during colonial times, all established plants are presumed to have been infertile (Greathead, 1976). We were able to collect *O. europaea* ssp. *cuspidata* and its primary tephritid pest, *B. oleae*, in various habitats and over a substantial range of altitudes throughout the forested areas of southern Kenya. This olive species was found in *Croton-Brachylaena-Calodendrum* Forest (Beentje, 1990), represented in our study by Ololua Forest (Fig. 1). It was also collected on Mt. Elgon in *Juniperus-Nuxia-Podocarpus* Forest (Beentje, 1990), and in Burguret Forest on the western slope of Mt. Kenya, an example of *Juniperus-Olea* Forest (Beentje, 1990). The collections made in Mau Forest were in a highly disturbed site of what probably had been a stand of *Juniperus-Olea* Forest.

The fruiting period of *O. europaea* ssp. *cuspidata* was not always clearly defined. In Ololua Forest, olives and *B. oleae* were found in abundance during three consecutive months between the short and long rainy seasons in 2000. Like *C. niloticus* in western Kenya, *Olea* fruits were absent (except in insignificant numbers on very few trees) in Ololua Forest during 2001 and 2002. In contrast, Burguret Forest produced ripe fruits over the 7-month period in which we sampled there, and many trees had green fruits during the final sampling date (November 2002) suggesting that fruiting may be year round in this location. Although only sampled on two occasions in Mau Forest, west of the Rift Valley, fruits of *O. europaea ssp. cuspidata* were collected at markedly different times of the year (September and February) and seasonality may be absent there as well. Our observations on the lack of an annual fruiting season in at least one population of *O. europaea* ssp. *cuspidata* recall the difficulties involved in a previous collection expedition to Kenya in 1975 when, despite using herbarium records as a guide to likely fruiting periods, Greathead (1976) was unable to find any olive fruits over two months of searching. A more rigorous longitudinal study of fruiting phenology of *Olea* species is necessary to determine whether patterns, if any, in fruit production exist in the wild.

Available quantitative data on development of olive fly in wild hosts is limited and, as noted by Neuenschwander (1982), often not readily accessible (e. g., Greathead, 1976). Our samples of mature fruits of *O. europaea* ssp. *cuspidata* were almost always (88.9%) infested, despite the irregular nature of the fruiting cycle at most sites. Infestation indices (mean 613.2 adults per kg ripe fruit, range 18–2833) were generally higher than those reported by Greathead (1976) for his samples (mean 81.3, range 1–410) from the same host plant in Ethiopia. Neuenschwander (1982), working in South Africa, found that many wild olive trees suffered no apparent attack by *B. oleae* but a few trees were heavily infested. Large collections of olive fly were previously obtained from wild olives in Kenya in 1949 (Clausen *et al.*, 1965) as part of a biological control program. Reported infestation rates (approximately 77,000 puparia from 100 gallons of olives) are difficult to compare with our collections.

The collections made at over 2800 m in Mt. Elgon forest represent the highest recorded observations of both the host fruit and olive fly. Previously, herbarium records (East African Herbarium,

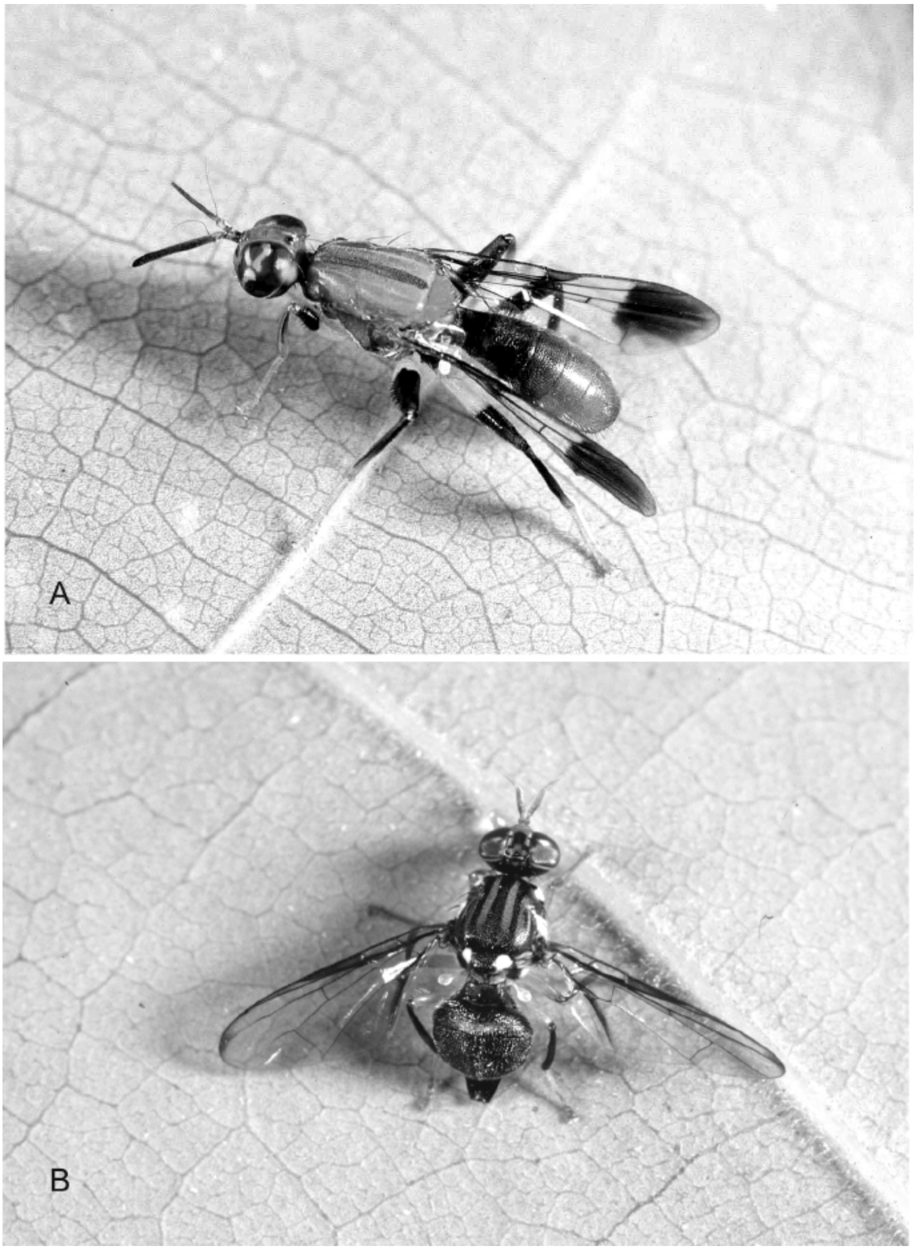

Figure. 8. **a**. *M. whartoni*, male habitus, live specimen; **b**. *B. munroi*, female habitus, live specimen.

National Museums of Kenya) indicated 2400 m as the highest collection record for *O. europaea* ssp. *cuspidata* (Beentje, 1994). Our collections on Mt. Elgon encompassed an altitudinal range of 2801–2979 m, nearly 600 m higher than the previously recorded maximum. This range may contain the absolute maximum altitude at which *B. oleae* is able to breed. Olives collected at the higher altitude failed to produce *B. oleae* while the collection made at 2801 m on the same day and another made three weeks later at 2809 m were infested (Table 2).

The discovery of *B. munroi* represents only the second *Bactrocera* species known to infest *O. europaea* s.l. Although the collections produced small numbers of *B. munroi* (Table 2), our rearing results show that it has a wider range of hosts than its congener *B. oleae*. In addition to its presence in samples from *O. europaea ssp. cuspidata* (where it co-occurred with *B. oleae*) it also developed in fruits of *O. welwitschii* and *Prunus africana*, from collections made in remnant, wet Guineo-Congolian forest in Kakamega. Production of *B. munroi* from *Prunus* was somewhat surprising, since the Rosaceae are not closely related to the Oleaceae (Soltis *et al.,* 2000). Although two different collections (13.iv.1999, 29.iii.2000) of *P. africana* produced five specimens, rearings from this fruit should be reconfirmed. Nonetheless, the wider host range of *B. munroi* and its occurrence in very different forest types suggest that its range in sub-Saharan Africa will exceed that of *B. oleae*, perhaps extending far into the equatorial rain forest belt to the west.

Is *B. munroi* a potential pest of commercial olive? Although this species clearly ranks far below *B. oleae* as a pest of wild olive in Kenya (it was present in 11.1% of the samples of ripe *O. europaea* ssp. *cuspidata*, while *B. oleae* was present in 88.9%), it is impossible to predict its potential as a pest on cultivars of *O. europaea* ssp. *europaea*. *Bactrocera oleae* itself is apparently a less important pest on cultivated olive in South Africa than in the Mediterranean Region (Neuenschwander, 1982; Hancock, 1989), perhaps because of the greater abundance of natural enemies in South Africa (Neuenschwander, 1982). Additionally, commercial olive is a far different fruit in both size and texture from wild olive (*O. europaea* ssp. *cuspidata*) and development of *B. munroi* might be more (or less) favored by a host switch of this kind.

Bactrocera biguttula was previously known only from South Africa. There it has been reared from the fruit of 3 plant species, all Oleaceae. Munro (1924) reared *B. biguttula* from *Olea woodiana* Knobl. ssp *woodiana*, *Chionanthus foveolatus*, and *Olea capensis* L. ssp. *capensis*. In Kenya, we reared *B. biguttula* from *O. woodiana* ssp. *disjuncta*, the only *Olea* or *Chionanthus* found in coastal lowland habitats. However, *C. battiscombei* is found in Coast Province, Kenya at altitudes as low as 850 m and it would be interesting to collect fruits from this population to see if *B. biguttula, Munromyia* species, or both develop in them.

Tephritidae were only reared from Oleaceae in the tribe Oleeae, subtribe Oleinae. While our sole representative of Oleeae, Schreberinae has a woody fruit and was not expected to yield fruit flies, it is noteworthy that none of the 17 collections of *Jasminum* species (tribe Jasmineae) produced Tephritidae. Although we can only speculate as to the reasons for this absence, it is probable that some feature of ripe *Jasminum* berries is not suitable for larval development of fruit flies. Fruits from all of our *Jasminum* collections were extremely aqueous and consistency of the mesocarp may be a factor. In contrast, the crambid larvae that developed in *Jasminum* possess mechanisms for exploiting this substrate.

While numerous parasitic Hymenoptera (Parasitica) were reared from olives, our rearing program was not designed to associate unequivocally with their hosts either the ectoparasitoids or those that pupated inside the fruit. They have thus been excluded from the dataset in Table 3. Species of ectoparasitoids included members of the genus *Eupelmus* (Eupelmidae) and *Bracon* (Braconidae). Both *Eupelmus* and *Bracon* contain species that are well known as parasitoids of olive fly, and Neuenschwander (1982) found *Bracon celer* (Szépligeti) to be the most abundant parasitoid of olive fly in his collections from South Africa. *Bracon celer* was reared from olives collected from Burguret Forest, where it was the third most common species of parasitoid, and was undoubtedly attacking *B. oleae*. It was rare or absent in samples from other sites. Many Eurytomidae were also reared from olive samples, but at least some of the species in this family are known to be phytophagous on olive seeds and some are also parasitoids of other chalcidoids in olive fruits.

Three species of endoparasitoids were reared from olive fly puparia, and host associations could thus be confirmed. All 3 belong to the braconid subfamily Opiinae, which are exclusively koinobiont endoparasitoids of cyclorrhaphous Diptera (Wharton, 1997, 1999). Where parasitoids were abundant, *Psyttalia lounsburyi* was the dominant species, followed by *Utetes africanus*. *Psyttalia concolor* was rarely seen in olives, though a species indistinguishable from *P. concolor* was commonly reared from the *Ceratitis capitata* in coffee in the central highlands (Wharton *et al.*, 2000). All three species have previously been reared from olive fly.

Psyttalia lounsburyi is known only from Kenya and South Africa (Silvestri, 1913; Clausen *et al.*, 1965; Neuenschwander, 1982). *Utetes africanus* is also known from these two countries, but has also been collected in Eritrea. Individuals from Eritrea are generally darker and were recognized as *U. africanus* var. *orientalis* Silvestri (1913). This dark form is the one we have reared in Kenya. Silvestri (1913) noted briefly that *U. africanus* attacks the larval stage of its host and emerges from the puparium. Additional details of the biology of these two species have yet to be published, but a culture of *P. lounsburyi* has been established in Nairobi from our samples and it also oviposits in larval stages of the host (S. Mohamed, pers. comm.). Details on its biology will be published separately.

Our samples suggest that the high elevation forests of Kenya will be good sources of natural enemies of olive fly for use in classical biological control programs. The complex of parasitoids in Kenya is sufficiently different from that found by Neuenschwander (1982) in South Africa to warrant collections from both countries. Rates of parasitization in our samples (Table 3) are consistent with the roughly 10% found by Clausen *et al.* (1965) in 1949, though there was considerable between-sample variation. Clausen *et al.* (1965) did not separate the species of opiines that they reared, so it is not possible to determine if the relative abundance of the three species we reared was the same as in their samples. However, examination of voucher material in the USNM (by RAW) indicates that the same species were reared.

Frugivorous Lepidoptera were more diverse in the Oleaceae than were Tephritidae, although infestation levels were much higher for the fruit flies. A similar pattern was found for insects attacking non-oleaceous fruits (n = >750 species) during this project (R. Copeland, unpubl. data). Lepidopteran species and their parasitoids make up a high percentage, and yet relatively poorly known component, of the guild of frugivorous insects. Previously, *Carposina chersodes* (Meyrick) (Carposinidae) and the common orchard fruit pest *Cryptophlebia leucotreta* (Meyrick) (Olethreutidae) were reared from *Olea europaea* ssp. *cuspidata* in eastern Africa (Greathead, 1976) and, in South Africa, Munro (1924) reported *Hendecasis* sp. from *Chionanthus foveolatus* and *O. woodiana* ssp. *woodiana.*

Fruits of the Oleaceae provide one example of the diversity of insects exploiting a largely overlooked larval resource. While the literature on forest herbivores is, by comparison, voluminous, little attention has been paid to the guild of frugivorous insects and their natural enemies. There may be several reasons for this. Certainly it is easier to consistently find leaf eaters in evergreen and, for that matter, deciduous tropical forest, whereas the search for fruits must be timed with greater precision. And fruits, such as those described in this report, may also be less seasonably reliable. However, while the insect fauna associated with leaves and stems is much richer than that of insects exploiting fruits, the latter comprise a significant portion of tropical insect biodiversity and deserve much closer attention.

Acknowledgments

We thank Dr. Richard Bagine, Kenya Wildlife Service, for granting us permission to sample fruits within Kenyan National Park forests. The Brooks family of Koru, Kenya kindly allowed us access to their property. We thank Rose Justus, Asha Nassor, and Augustus Hare for their excellent work in overseeing the handling of so many fruits and flies in our rearing facilities. Mathias Ngonyo, Wilberforce Okeka, and Juliet Muriuki were invaluable field assistants. Quentin Luke of the East African Herbarium provided expert plant identifications. We thank the Director General, ICIPE, for providing office and laboratory space and a field vehicle for this project. We are grateful to Dr. Scott Miller, Head, Department of Systematic Biology, National Museum of Natural History, Smithsonian Institution,Washington, D.C. for arranging for library services. Scott Miller and Koen Maes provided identifications of Lepidoptera and Mike Gates identified the Chalcidoidea. Allen Norrbom assisted RSC in many ways and Lucrezia Rodriguez and Linda Lawrence helped with the figures.

This work was supported primarily by USAID grant No. PCE-G-00-98-0048-00 (in collaboration with the International Centre of Insect Physiology and Ecology and its African Fruit Fly Initiative) and in part by USDA/CSREES/IFAFS grant No. 00-52103-9651, both to Texas A&M University.

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Biogeography and Speciation in the Dacini (Diptera: Tephritidae: Dacinae)

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Abstract

The geographic distributions and host associations of the Dacini in the area from the Indian subcontinent, through South East Asia to Papua New Guinea and the South Pacific, are discussed. Included in this is the biogeographic significance of Wallacea and more detailed analysis of the Papua New Guinea and Australian fauna in relation to the rainforest flora of the same region. In summary, it is postulated that the Dacini species have cospeciated with rainforest plant species in a process fitting the Recognition Concept of species (Paterson, 1985). Although the tropical and subtropical rainforest flora are Gondwanan in origin, the Dacini fauna appear to have speciated primarily over the Tertiary Period, influenced by a combination of oscillations in topography, localized climate and land bridges during glaciation cycles.

Introduction

The Dacini, primarily comprised of species of 2 genera (*Bactrocera* Macquart and *Dacus* Fabricius), form a major part of the tropical and subtropical Tephritidae. In the Asian, South East Asian to Pacific region in particular, there has been extensive speciation. The occurrence of large numbers of sibling species, the patterns of distribution of fly species and their endemic host plants, and the strong biological relationship of species to their host plants, provide a unique opportunity to study the biogeography and speciation within this important group of flies. In this paper, a discussion of biogeography and speciation is presented from taxonomic and ecological perspectives. Hopefully, as molecular techniques advance and phylogenetic research is undertaken for large numbers of dacine species, this paper will provide some useful baseline information.

Species – The Fundamental Problem

Species are real entities, each having its own genetic makeup and usually regarded as a unit of evolution. For the taxonomist, the basic challenge is to define (and name) species in a way that will provide an understanding of their nature and origin. In other words, in the Dacini, we need to know if there is a relationship between the morphological characterizations and the real unit of evolution. This is particularly relevant when we see that large numbers of sibling species occur. What, then, is the most significant concept of species within the group that, in turn, will provide accurate species definitions?

From a practical viewpoint, dacine taxonomy began with pure morphological definitions of species and this proved satisfactory until we encountered the extensive speciation that has led to the large groups of sibling species (e.g., May, 1951, 1965; Hardy, 1951, 1973, 1974; Drew, 1989). In an attempt to elucidate the species within the *Bactrocera dorsalis*-complex of South East Asia, Drew and Hancock (1994) used host plant records, male pheromone chemistry and some molecular data to help separate the most difficult populations. In many cases, the biological and chemical data have been extremely helpful, to date, but DNA analyses have not provided definitive solutions.

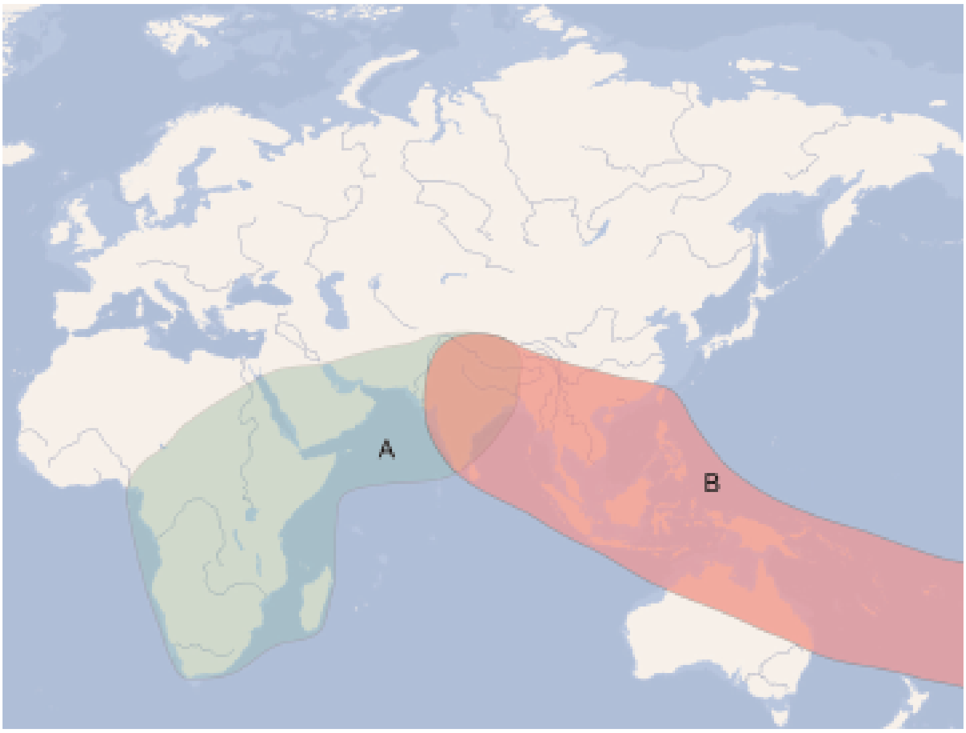

Figure 1 – The endemic distribution of Genus *Dacus* Fabricius (A) and Genus *Bactrocera* Macquart (B). Note some overlap in the area of the Indian subcontinent.

Geographic Distributions of Dacini Species

The worldwide distributions of known species within the tribe Dacini is given in Table 1. Based on current available data, there are 880 described species of which 629 belong to the genus *Bactrocera* and 248 to the genus *Dacus*. The endemic distributions of the genera *Dacus* and *Bactrocera* are shown in Figure 1. All but 10 of the *Bactrocera* are distributed in the region from India, across South East Asia to the Pacific Islands whilst the majority of *Dacus* species belong to the African continent.

Within the Asian-Pacific Dacini, primarily consisting of *Bactrocera* species, the largest number of species occur in South East Asia and Papua New Guinea. Westwards from South East Asia, to India and surrounding areas (countries) the number of species declines. Similarly, east and southeast from South East Asia and Papua New Guinea, the number of species declines. In this direction, a distinct filtering effect across islands can be observed (Table 2). This effect could be related to the decline in land area of the islands with longitude, in an easterly direction, or a combination of this and the reduced areas of rainforests that also follow the same pattern.

Endemism. For this analysis, endemic species are defined as those that occur within the specific region only. This eliminates those that are shared and those that have been more recently introduced. The percentages of species in each major genus, endemic to the Indian subcontinent, South East Asia, Papua New Guinea, Australia and the Pacific islands are listed in Table 3.

The high levels of endemism in each area indicates that speciation has occurred in relative isolation over a considerable period of time. The lower level of endemism in India, with 23 species occurring in common with South East Asia, indicates a level of contact between these 2 zones. There are 13 species shared between Australia and Papua New Guinea and 6 species shared between Papua New Guinea and South East Asia. Probably, these zones have been isolated for a very long period

Table 1. Worldwide geographic distribution of species of Dacini in each of the four genera

	Total No. Species	Bactrocera Species	Dacus Species	Ichneumonopsis	Monacrostichus
Africa (incl. Madagascar and Mascarene Is)	182	10	172	0	0
Indian Subcontinent	68	56	12	0	0
Southeast Asia	256	218	35	1	2
Papua New Guinea	180	167	13	0	0
Australia	88	76	12	0	0
Solomons (incl. Bougainville)	53	51	2	0	0
Vanuatu	12	11	1	0	0
New Caledonia	11	10	1	0	0
Fiji	4	4	0	0	0
Tonga	6	6	0	0	0
Samoa	7	7	0	0	0
Niue	2	2	0	0	0
Cook Islands	2	2	0	0	0
Austral Islands	2	2	0	0	0
Society Islands	2	2	0	0	0
Marquesas Islands	1	1	0	0	0
Tuamotu Archipelago	2	2	0	0	0
Micronesia/N. Pacific	2	2	0	0	0
Totals	880	629	248	1	2

Table 2. Percentage of known species of Dacini (Diptera: Tephritidae: Dacinae) in major geographic areas

Country	Percent of total fauna
India	10.0
South East Asia	37.0
Papua New Guinea	26.0
Australia	13.0
Solomon Islands	8.0
Vanuatu	2.0
New Caledonia	2.0
Fiji	0.4
Tonga	0.7
Western Samoa	0.8
Other South Pacific Islands	0.1

Table 3. Percentages of species of Bactrocera and Dacus endemic to each major geographic area

Genus	Indian Subcontinent	SE Asia	PNG	Australia	Pacific Is.
Bactrocera	66	89	90	84	100
Dacus	67	86	92	92	100

with a longer break between Papua New Guinea and South East Asia. For the Dacini, the line of demarcation between the endemic Papua New Guinea fauna and that of South East Asia appears to be the eastern part of Wallacea, i.e. further east than Wallace's line. Another point to note is that there is very little difference between the percent endemism in the genus *Bactrocera* and genus *Dacus* in each zone. Although *Dacus* has been through more prolific speciation in Africa, Drew and Hancock (2000) suggested that the parent stock of all Dacinae are Gondwanan in origin and arose in the area now known as India rather than the Southeast Asian/Australasian plate. Indeed, the Asian *Dacus* subgenera *Callantra*, *Dacus* and *Didacus* appear to have arisen from the same parental stock, taking into account the endemic host plant families that they have in common. One can conclude that the Asian-Pacific *Bactrocera* and *Dacus* have been actively speciating, concurrently, for the same time period.

Geographic Distribution of the *Bactrocera dorsalis*-complex Species

During the past 2 decades, we have had extensive male lure trapping and host plant surveys across South East Asia, Papua New Guinea, Australia and the South Pacific Islands. This has resulted in detailed knowledge of the *Bactrocera dorsalis*-complex species and their geographic distributions over a wide area. Currently, the *dorsalis*-complex is known to consist of approximately 80 described species and another 20 undescribed which are held in our collections. The data summarized in Table 4 are based on the 80 species described in literature.

The low numbers recorded in Myanmar, China, Laos and Cambodia have resulted from collections not being conducted in these countries. In Peninsular Malaysia, Thailand and Vietnam, approximately 80% of species are shared.

Using the *dorsalis*-complex as an indicator, one can conclude that the real "hot spots" of dacine speciation have been the present continental area surrounded by Thailand, Vietnam and Peninsular Malaysia and the isolated land areas of the Philippines, Indonesia, "Borneo" and Papua New Guinea. Probably, the Philippines, Indonesia and Borneo are more recent separations from the continental

Table 4. Geographic distribution of sibling species within the dorsalis-complex (Diptera: Tephritidae: Dacinae) from the Indian subcontinent, South East Asia to Australia

Country	No. Species
Bhutan	1
Bangladesh	1
Nepal	1
Pakistan	1
India	4
Sri Lanka	3
Andaman Islands	2
Myanmar	1
China	1
Taiwan	1
Laos	1
Cambodia	2
Vietnam	17
Thailand	14
Palau	1
Philippines	13
East Malaysia, Brunei, Kalimantan	10
Peninsular Malaysia	18
Singapore	7
Indonesia	19
Christmas Island	2
Papua New Guinea	15
Australia	4

area and that this occurred after the majority of speciation was complete. Supporting this hypothesis is the presence of a number of rainforest-based *dorsalis*-complex species common to Thailand, Vietnam, Peninsular Malaysia, Indonesia and "Borneo". The Philippines possess some endemic species in the complex, probably resulting from a longer period of isolation than that for Indonesia, "Borneo" and Papua New Guinea.

Host Plant Relationships

Over the past 2 decades there has been considerable research into adult fly feeding, courtship and mating behavior (e.g., Drew et al., 1983; Drew & Romig, 2000; Drew & Lloyd, 1987; Fletcher et al., 1978; Green et al., 1993; Prokopy *et al.*, 1996). All studies showed that adult feeding, courtship and mating occurred on the host plants. Flies visited host plants and fed when fruit were at a developmental stage just prior to being susceptible to oviposition while courtship and mating occurred as the fruit entered the susceptible stage. A recent study on *Bactrocera cacuminata* (Hering) contradicting this extensive earlier research (Raghu *et al.*, 2002) has now been shown to be incomplete as the primary study was conducted over a very short period (December) of the entire 8-month fruiting cycle of the host plant, *Solanum mauritianum* Scop. Subsequent recordings of matings of *B. cacuminata* in 2 host plants from September 2002 to April 2003 showed that they began in early October (second month of Spring), peaked in mid-November (with 27 mating pairs on one night) and ended in late-November at which stage almost all fruit had fallen. In December when the work of Raghu *et al.* (2002) was conducted, there were post-teneral (immature) adults in the host plants that emerged from pupae from the earlier fallen fruit.

From 1986 to 1991, we conducted extensive host fruit collecting in rainforest habitats in South East Asia. Over 30,000 samples were taken and the records published by Allwood *et al.* (1999). From the mid-1970s to 1998, I established extensive host collecting in eastern and northeastern Australia, firstly with specific research projects and later with the *B. papayae* eradication program. These records have been published by Hancock *et al.* (2000). Further analyses of these data show an interesting pattern in the utilization of endemic host plants of endemic fly species (Table 5 and 6).

In both Australia and South East Asia, a similar percentage of *Bactrocera* species are monophagous (37 and 33 percent, respectively). Similarly, 21 and 14 percent respectively are polyphagous with 12 or more endemic host plant species. Most pest species are polyphagous in their native rainforest habitat, breeding in a large number of plant species in many plant families. (Note: In India, Sri Lanka and the Philippines, there has not been extensive host fruit collecting and so the records for the pest species, *B. caryeae*, *B. kandiensis*, *B. occipitalis* and *B. philippinensis*, are deemed incomplete). Also, a few pest species are specialists, e.g. *B. cucumis* (primarily breeding in Cucurbitaceae species), *B. minax* (in citrus), *B. musae* (in *Musa*), *B. pyrifoliae* (in Rosaceae) and *B. umbrosa* (in *Artocarpus* spp.). *Dacus* species in the South East Asian and Pacific regions have limited host ranges (Tables 5, 6) and none has developed to significant pest status.

At the plant family level, 67% of *Bactrocera* species in South East Asia and 50% in Australia utilize hosts in one family only. An example is the *Bulladacus* species recorded from India, through South East Asia, Papua New Guinea to Samoa in the central South East Pacific. All species over this area have evolved in species of Gnetaceae.

With our knowledge of the strong fly-species/host-plant behavioral relationships, the consistent patterns of monophagy and polyphagy across biogeographic regions and speciation within single plant families, we can propose with some confidence, that a process of cospeciation or coevolution has existed [see Page (2003) for definitions of cospeciation and coevolution].

Geological Background

The break-up of Gondwana led to an eventual collision of India with Asia. This resulted in an influx of Gondwanan flora into Asia and explains why there are strong botanical relationships, at the generic level, among the rainforests of Australia, Papua New Guinea, parts of South East Asia and India. However, Hall (1998) stated that the present distribution of plants (and animals) in South East Asia might owe much more to activities of the last 1 million years than the preceding 30 million years.

Table 5. Number of endemic plant taxa recorded as hosts of endemic fruit fly species (Diptera: Tephritidae: Dacinae) in South East Asia

Fruit Fly Species	No. Plant Families	No. Plant Genera	No. Plant Species
Genus Bactrocera			
atrifemur	1	1	1
apicalis	1	1	1
calophylli	1	1	1
caudata	1	1	1
cilifera	1	1	1
kinabalu	1	1	1
lata	1	1	1
maculifacies	1	1	1
matsumurai	1	1	1
mcgregori	1	1	1
munda	1	1	1
nigrotibialis	1	1	1
quasipropinqua	1	1	1
rubella	1	1	1
rubigina	1	1	1
thailandica	1	1	1
trilineata	1	1	1
verbascifoliae	1	1	1
versicolor	1	1	1
dorsaloides	1	1	2
melastomatos	1	1	2
trimaculata	1	1	2
garciniae	1	1	4
umbrosa	1	1	4
propinqua	1	1	8
abbreviata	1	2	2
kanchanaburi	1	2	2
scutellata	1	2	2
arecae	1	2	3
depressa	1	2	3
isolata	1	2	7
tsuneonis	1	2	7
minax	1	2	8
hochii	1	3	3
scutellaris	1	3	4
osbeckiae	1	3	6
hyalina	1	4	5
diversa	1	6	9
kandiensis	2	2	2
limbifera	2	2	2
occipitalis	2	2	2
pendleburyi	2	2	3
irvingiae	3	3	3
pyrifoliae	3	3	3
philippinensis	4	4	4
sp.n. (not incisa)	4	4	4
raiensis	4	4	5
caryeae	5	5	5
tuberculata	6	8	9
albistrigata	7	7	10
tau	7	19	32
latifrons	8	9	20
cucurbitae	10	22	36
zonata	12	13	13
correcta	22	36	50
carambolae	24	44	68
dorsalis	31	65	97
papayae	45	100	166
Genus Dacus			
esakii	1	1	1
polistiformis	1	1	1
sphaeroidalis	1	1	1
longistylus	1	1	2
keiseri	1	2	2
longicornis	1	3	4
ciliatus	1	5	6
Genus Monacrostichus			
malaysiae	1	1	1
citricola	1	1	6

Table 6. Number of endemic plant taxa recorded as hosts of endemic fruit fly species (Diptera: Tephritidae: Dacinae) in Australia

Fruit Fly Species	No. Plant Families	No. Plant Genera	No. Plant Species
Genus Bactrocera			
aeroginosa	1	1	1
alyxiae	1	1	1
aurea	1	1	1
bancroftii	1	1	1
bidentata	1	1	1
calophylli	1	1	1
chorista	1	1	1
decurtans	1	1	1
diospyri	1	1	1
ektoalangiae	1	1	1
hispidula	1	1	1
humilis	1	1	1
melas	1	1	1
mendosa	1	1	1
parabarringtoniae	1	1	1
phaleriae	1	1	1
pulchra	1	1	1
robiginosa	1	1	1
breviaculeus	1	1	2
tigrina	1	1	2
visenda	1	1	2
fagraea	1	1	3
expandens	1	1	4
tenuifascia	1	2	2
pallida	2	2	2
barringtoniae	2	2	2
turneri	2	2	2
signatifera	2	2	3
aglaiae	2	2	3
aberrans	2	4	6
opiliae	3	3	3
mayi	3	4	7
bryoniae	3	5	6
murrayi	4	4	4
laticaudus	4	5	5
rufofuscula	4	5	7
musae	5	5	5
nigra	5	6	6
cacuminata	6	6	6
manskii	6	6	6
cucumis	6	6	8
endiandrae	6	9	23
aquilonis	7	10	13
halfordiae	8	10	12
jarvisi	15	19	33
kraussi	27	43	74
neohumeralis	36	59	91
tryoni	39	73	133
Genus Dacus			
(Callantra) axanus	1	1	2
(Dacus) absonifacies	1	1	1
(Dacus) secamoneae	1	1	1
(Didacus) aequalis	1	1	1
(Didacus) hardyi	1	1	1

This statement could also be applied to the Australian Region where our fossil records indicate establishment of Diptera and active speciation during the late Quaternary, especially associated with glaciation cycles over the past 150,000 years.

We can conclude that the break-up of Gondwana laid the foundation through the distribution of established rainforest habitats within which active speciation of, at least, the genus *Bactrocera* could later occur. Hall (2001) emphasized that the geological understanding of a region is useful in elucidating its biogeography but may only provide an essential background to what is a complex process of evolution. That is, other processes have, more recently, influenced speciation. For example, geologically induced changes in topography and localized climate, together with changes in land bridges during the glaciation cycles, have directly influenced speciation processes. The extensive island systems throughout South East Asia and the South Pacific region experienced these glaciation-induced changes and this laid a fertile ground for speciation in the Dacini.

Biogeography of Rainforests

Given that the endemic habitat of the Dacini is the rainforest ecosystem of the tropics and subtropics, we need to analyze the distribution of this flora. Basically, the Indomalayan rainforests (tropical rainforests in contrast to Temperate rainforests) occur in a band that includes the Indonesian archipelago, the southern Thailand isthmus, Malaysia and Papua New Guinea. In addition, there are current outlier groups in northwestern and southeastern Thailand, Indo-China (especially Vietnam), southern China, Philippines, Borneo, the Andaman Islands, southwest Sri Lanka and the Western Ghats of southwest India. Elements of the same tropical rainforests also extend to northeastern Australia, the Melanesian archipelago (Solomon Islands, Vanuatu, Fiji, Samoa, Tonga) and into Micronesia and Polynesia (Whitmore, 1986). In all of these locations, species of Dacini are endemic.

These rainforests have many endemic Dacini host plant families that date back to the Cretaceous and Tertiary Periods (Cronquist, 1981). They are extremely rich in number of species, due to considerable localization of evolution at the species level (Whitmore, 1986) and contain large numbers of plant sibling species and endemic plant species with localized distributions. The numbers of rainforest plant species decline from S.E. Asia to Papua New Guinea, and then markedly to Australia and the South Pacific Islands. Drew and Hancock (2000) proposed that the dacine species and their host plants have continued to coevolve over the Tertiary and Quaternary Periods.

Case Study – The Australian Region

Because of a reasonably comprehensive knowledge of the biogeography and ecology of the rainforest flora in the Australian region (Webb & Tracey, 1981; Barlow, 1981) combined with sound geological assessments (Hall, 1998, 2001), the biogeography and speciation in the Dacini in this zone can be discussed in more detail. Also, the broad area of biogeographic transition, called Wallacea, forms a zone of differentiation between South East Asia on the one side (Sundaland) and Australia/Papua New Guinea on the other (Hall, 2001). Wallacea was first recognized by Wallace (1869) and is bound by Wallace's Line running between Bali and Lombok in the West and Lydekker's Line east of Timor and Seram (Figure 2). Consequently, Wallacea includes Lombok and islands in the Indonesian archipelago to the East, Timor, Kai Island, Sulawesi and the Moluccas (which include Seram, Buru and Halmahera), localities from which we have good records of Dacini, in addition to the extensive records in Papua New Guinea, Australia and other Indonesian islands.

The rainforests of Australia are comprised of a series of pockets along the East coast and across parts of the northern coastline, separated by dry corridors. Prior to European settlement these forests covered approximately 1% of the total Australian land surface compared with 100% in Papua New Guinea, 32% in the neotropics and 9% in Africa.

Although the forests are Gondwanan in origin and date back to the Cretaceous, the distribution patterns at present are estimated to be some 4,000–12,000 years old (Webb & Tracey, 1981). They possess an Indomalayan element, as do those of Papua New Guinea and contain many Dacini host plants. We have recorded some 56 plant families in Australia and 65 families in South East Asia (Allwood *et al.*, 1999; Hancock *et al.*, 2000) that contain host plants of *Bactrocera* and *Dacus* species.

Figure 2. The biogeographic region of Wallacea, bounded by Wallace's Line in the West and Lydekker's Line in the East.

Four glaciation periods have been recorded during the late Quaternary and these resulted in climatic oscillations, ecological differentiation and periods of geographical isolation, leading to considerable speciation in the forests (Webb & Tracey, 1981).

Papua New Guinea and Australia were joined into a large and ecologically diverse continent until the end of the last glaciation, 10,000–8,000 years ago. (Webb & Tracey, 1981). The rainforests of Papua New Guinea, after separation, must have experienced a more humid, moist and higher temperature climate than their counterparts in Australia as they covered most of the land area and underwent more prolific speciation. It is also believed that Papua New Guinea received considerable floristic influence from the Malaysian region at the end of the Oligocene Period, at the same time as Australia joined to Sundaland (Barlow, 1981).

During the late Tertiary, Australia was in contact with the Indomalayan region (Barlow, 1981) and today Wallacea contains elements of both the South East Asian and Australian-Papua New Guinea floras, in addition to its own endemic species.

The numbers of plant species and areas of land covered by these rainforests decline markedly with increasing distance South and East from Papua New Guinea. A comparison of the rainforest communities between Papua New Guinea and Australia provides valuable background information. The current estimates of numbers of rainforest plant genera and species are as follows (data provided by Queensland Herbarium) –

	Papua New Guinea	**Australia**
No. Genera	716	545
No. Species	8000	1600

The following are significant features of the rainforest floras of Papua New Guinea and Australia –

- There are close relationships at the generic level, indicating a common phylogenetic ancestry.
- There are low numbers of shared species and large numbers of endemic species, suggesting more recent speciation uninfluenced by migration. This speciation has been more vigorous in Papua New Guinea than Australia.
- There is some evidence of close relationships between the 2 areas at the species level when comparing similar environmental ecosystems.
- Within Australia, the composition of the flora changes markedly from North to South along the East coast.
- The Papua New Guinea and Australian floras are probably the result of long climatic sifting of a single ancestral stock. Superimposed on this is the impact of the Indomalayan element which has formed a significant part of the Papua New Guinea flora but not the Australian flora.
- During the last glacial period, the PNG-Australia land bridge would have been as arid as is that area adjacent to the Gulf of Carpentaria today and which separates, ecologically, northeastern and northwestern Australia.

A comparison of the dacine fauna of Papua New Guinea, northeastern and northwestern Australia shows features similar to the floristic patterns. These 3 areas are currently ecologically isolated, one from the other, and the number of endemic dacine species known to occur are as follows:

Papua New Guinea — 164 species*
Northeastern Australia — 70 species
Northwestern Australia — 7 species

*(Our recent extensive surveys in PNG have collected at least 50 more undescribed species not included here).

The following observations can be made:

- The endemic dacine faunas of Papua New Guinea and Australia are each unique and different.
- There is a low level of similarity between all three areas in species character states and with only a few species shared.
- In general, there is little change in species distributions with altitude.
- Within Australia most species occur in the northeastern area and there is marked decline in numbers of species from North to South along the eastern coast.
- The distributions of genera and species of both the rainforest flora and dacine fauna show considerable similarities.

The Dacini fauna within Wallacea has been reported by Hardy (1982, 1983), Drew and Hancock (1994) and Drew *et al.* (1998). There are 37 species endemic to Wallacea, 11 shared with South East Asia, 6 shared with Irian Jaya/Papua New Guinea and 2 with Australia.

Generally, the character states of the endemic species show more relationship with species in South East Asia. Based on these data, Wallacea, as well as being a transitional zone has experienced considerable independent speciation.

Speciation – Process and Concept

The extensive speciation, particularly in the Genus *Bactrocera* throughout Asia, South East Asia and the Pacific, appears to have proceeded within the rainforest habitat. Further, the fly species have probably evolved in association with speciation of the flora. The question remains – what are the influences on the processes of speciation in the Dacini?

Hall (1998) stated that "no single factor will account for the distribution of plants and animals in South East Asia. Tectonic movements may be a control but their importance is still far from clear".

As noted above, there is a strong relationship between a dacine species and its host plant to a point where courtship and mating occurs within the host species. Consequently, evolving host plants and associated changes within the host environment would have a significant direct influence on the fruit fly species reproductive behavior. The term cospeciation as defined by Page (2003) as "the joint speciation of 2 or more lineages that are ecologically associated" could be applied here. Given that a fly population could cospeciate with its host plant and that many fly species have specific host plants, a number of such events could have proceeded simultaneously within separate fly lineages, in the same forest area. This concept, based on the "Center of Activity" model of dacine behavior, provides an understanding of how many species of fruit flies have arisen in the same continental land areas. Bush (1975) described this as sympatric speciation in his *Rhagoletis* studies. The tectonic movements, associated topographic changes, oscillations in climatic patterns, ecological and geographic isolations all led to long periods of independent evolution of rainforest plant taxa, large numbers of species and considerable endemism. This pattern of events could also have resulted in the large number of dacine species that we know today. Clayton *et al.* (2003) also recorded that changing ecological factors can have an influence on coevolution and cospeciation.

It is interesting to note that the large sibling species complexes, the *dorsalis*-complex and the *tau*-complex, contain some species with wide host ranges. It is possible that species such as or similar to *Bactrocera dorsalis* (Hendel) and *Bactrocera papayae* Drew & Hancock, with extensive host ranges in the rainforests, were the precursors of more than one lineage within the *dorsalis*-complex.

In speciation, population behavior and genetic changes must proceed simultaneously. In applying the isolation concept of Dobzhansky (1935) and Mayr (1963, 1970) to the Dacinae, it is difficult to assess the relative importance of genetic and habitat changes. Whether or not basic genetic changes are needed first is debatable. It has been proposed that if a segment (part) of a population becomes geographically isolated, one of 3 possibilities can result: survival, extinction, speciation.

Fruit flies appear to have the genetic capacity to survive climatic or environmental changes and thus such changes are more likely to influence behavioral divergence before genetic divergence. For Dacinae, the isolation concept of Dobzhansky and Mayr causes problems in that it begins with genetic changes leading to reproductive isolation. It leaves little scope for relating changes in the host plant environment to those in the insect population. Similarly it leaves no opportunity for understanding a relationship between the perceived isolating mechanisms and the habitat changes. Further, for the large number of sibling species of Dacinae to have developed over a region such as the Indonesian Archipelago where often only 1 species occurs per land unit (e.g. island), either these species evolved in sympatry and then the land units divided or the units of land divided and speciation was completed in allopatry without the need for reinforcement. In other words, it is difficult to imagine that over many islands, separation and reuniting always occurred in order to allow reinforcement. Probably, large fruit fly complexes such as the *dorsalis*-complex have originated in allopatry, after geographic or ecological isolation of the units of land or habitat.

The recognition concept of species (Paterson 1985) relates geographic isolation and habitat change to changes in the courtship and mating behavior of the population. Thus it accommodates changes or speciation in the rainforest habitat. Because dacine mating occurs on the host plant and mate recognition is dependent on the host, e.g. the release of pheromones while on the host during courtship, it seems plausible that plant speciation in the rainforests have influenced changes in mate recognition systems of fruit fly species. In this model, genetic changes in the fruit fly occur secondarily, induced by changes in host plant influences on fruit fly mate recognition systems. It is interesting that some sibling fruit fly species e.g. *B. tryoni* and *B. neohumeralis* reveal no detectable genetic differences in molecular and cytological studies (Morrow *et al.*, 2000).

The recognition system also forecasts that the rate and scope of speciation is inversely proportional to population size, i.e. widespread populous species are more evolutionarily inert. This relates to the Dacini where large numbers of sibling species occur in small populations over narrow geographical ranges.

Under the recognition concept, it has been predicted that more sibling species will occur in groups where the mate recognition systems are dominated by olfactory and auditory signals (i.e. non-visual signals). The extensive sibling speciation in the Dacini, which depend on olfactory and auditory mate recognition, also supports this theory.

In comparing the 2 concepts and their applicability to the Dacinae, it is clear that the recognition system is a better fit. A practical advantage of this system is that it leads us to place emphasis on certain biological characters for identifying sibling species. In particular, key factors in Mate

Recognition such as specific endemic host plants and male pheromones have been used and are essential for accurate species identifications. This is also applicable to allopatric populations of sibling species such as *B. tryoni* in eastern Australia and *B. aquilonis* in northwestern Australia. Such a valid species concept also guides biologists into researching important aspects of field biology. This is probably the major contribution of the recognition concept to taxonomists interested in understanding the biology of the organisms that they are studying. Pertinent biological characters for species identification assist in the evaluation of morphological characters that often reveal only minor differences.

Taxonomists depend heavily on morphological characters although they are often secondary signs of speciation. It is essential, therefore, to develop an understanding of the speciation process and related biological and reproductive processes that are the primary criteria in determining species. In the Dacinae, the Recognition Concept provides this opportunity.

Conclusions

Clearly, the Dacini fauna of the Asian, South East Asian and Pacific regions have speciated over the Tertiary Period in the rainforests that date back to Gondwana. The close ecological relationship between fruit fly species and their host plants, especially in the area of host plant based courtship and mating, would result in the fly speciation process being directly influenced by speciation in the flora. Consequently, prolific localized speciation in the forests across South East Asia and Irian Jaya/Papua New Guinea, in particular, has resulted in large numbers of species of Dacini, including groups of sibling species with significant differences in the endemic host plants that they utilize. Between South East Asia (Sundaland) and the Australian Region (Irian Jaya/Papua New Guinea through to the South Pacific Islands), the area called Wallacea forms a transitional zone with a large endemic fauna and a small number of species shared with either South East Asia or Papua New Guinea/Australia. The identification of habitat based mate recognition systems in the Dacini and the potential for allopatric speciation throughout the extensive island systems, support the Recognition Concept of species proposed by Paterson (1985).

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Bibliography of and New Taxa Described by D. Elmo Hardy (1936–2001)[1]

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Abstract

A complete list of the publications authored or co-authored by D. Elmo Hardy, including notes presented at meetings, is given in chronological order. Additionally, a complete list of the new taxa of Diptera described by Hardy is presented.

Introduction

Over his exceptionally long and productive career of 65 years, D. Elmo Hardy published over 437 articles and notes proposing 1,867 new species-group names in 34 different families of Diptera. His proclivity in publishing and describing species is amazing when one considers the amount of time Elmo spent each year traveling on sabbaticals, attending international meetings, visiting family on the mainland U.S. almost every Christmas, and still meeting his teaching responsibilities. We present here as complete a list as possible of every published item attributed to his authorship or co-authorship. We include his many published notes that were presented at various meetings of the Hawaiian Entomological Society. These were not listed by Elmo in his own tracking of his publications, but in many cases, new state records or other novel biological observations are included in those notes and no where else and thus are essential literature references.

A second section lists all new taxa (family-group, genus-group; species-group) that were proposed by Elmo as an author or co-author. The four major families that garnered his attention were Tephritidae (465 new species-group names), Drosophilidae (444), Pipunculidae (346), and Bibionidae (305); although Elmo is also well-known for his major contributions toward the Hawaiian dolichopodid fauna (109 new species-group names).

Lastly, an assessment of Elmo's contribution to Diptera taxonomy is presented in comparison to the top thirteen dipterists.

Complete List of the Scientific Writings of D. Elmo Hardy

The following is a complete listing of all printed articles and notes attributed to Elmo Hardy (either as author or co-author) giving full citation data as well as accurate dating of each publication. All dating of the *Proceedings of the Hawaiian Entomological Society* derives from Evenhuis (1995, *Proceedings of the Hawaiian Entomological Society* 32: 39–44). All other dating, if derived from sources outside the journal issue, are annotated. Boldface numbers are Hardy's numbering system [also used in his bibliography in *Beiträge zur Entomologie* 31: 3–11 (1981)]. Articles not numbered by Hardy are indicated by open brackets "[ ]". Co-authors are listed in boldface after the citation with Hardy indicated by "DEH".

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[1] Contribution no. 2003-019 to the Hawaii Biological Survey.

1936

1. A new Bibionidae (Diptera) from Utah. *Proceedings of the Utah Academy of Science, Arts and Letters* **13**: 195. [July 1936]

1937

2. New Bibionidae (Diptera) from Nearctic America. *Proceedings of the Utah Academy of Science, Arts and Letters* **14**: 199–213. [July 1937]

1938

3. New Therevidae (Diptera) from Utah. *Annals of the Entomological Society of America* **31**(2): 144–146. [29 June 1938]

5. Blood-sucking Utah Diptera. *Proceedings of the Utah Academy of Science, Arts and Letters* **15**: 103–105. [Co-authored: DEH, **Knowlton, G.F.** & **Harmston, F.C.**] [June 1938]

4. New Bibionidae from British Columbia. *Canadian Entomologist* **70**(9): 207–210. [5 November 1938]

1939

7. New Nearctic Pipunculidae (Diptera). *Journal of the Kansas Entomological Society* **12**(1): 16–25. [24 January 1939]

8. New and little known western Pipunculidae (Diptera). *Annals of the Entomological Society of America* **32**(1): 113–123. [Co-authored: DEH & **Knowlton, G.F**.] [20 March 1939]

6. New and little known Utah Pipunculidae (Diptera). *Canadian Entomologist* **71**(4): 87–91. [Co-authored: DEH & **Knowlton, G.F**.] [5 May 1939]

1940

9. Studies in New world *Plecia* (Bibionidae-Diptera). Part I. *Journal of the Kansas Entomological Society* **13**(1): 15–27. [January 1940]

10. Dorylaidae notes and descriptions (Pipunculidae-Diptera). *Journal of the Kansas Entomological Society* **13**(4): 101–114. [October 1940]

1942

11. A note on leafhopper abundance. *Journal of the Kansas Entomological Society* **15**(1): 34. [January 1942]

12. New western Asilidae. *Journal of the Kansas Entomological Society* **15**(2): 57–61. [April 1942]

13. Studies in New World *Plecia* (Bibionidae-Diptera). Part II. *Canadian Entomologist* **74**(6): 105–116. [19 June 1942]

14. [Supplementary material and figure. *In*: Johnson, D.E.] A new *Cyrtopogon* (Asilidae, Diptera) from Utah. *Great Basin Naturalist* **3**(1): 1–4. [30 June 1942]

[The title page of the article has “15 June”, but the reprint in the library at SI has “mailed June 30, 1942” printed at the top of the first page.]

15. Studies in New World *Philia* (Bibionidae). Part I. *Journal of the Kansas Entomological Society* **15**(4): 127–134. [October 1942]

16. Notes on Diptera in the Snow Entomological Collection. *Journal of the Kansas Entomological Society* **15**(4): 142–143. [October 1942]

1943

17. New Therevidae and Asilidae in the Snow Entomological Collection. *Journal of the Kansas Entomological Society* **16**(1): 24–29. [January 1943]

18. Studies in *Phyllomydas* (Mydaidae-Diptera). *Journal of the Kansas Entomological Society* **16**(2): 50–52. [April 1943]

19. Revision of Nearctic Dorilaidae (Pipunculidae). *Kansas University Science Bulletin* **29**(1): 3–231. [15 July 1943]

1944

21. Medical entomology in Assam, India. *China-Burma-India Theatre Medical Bulletin* **1944** (January): 1–44. [January 1944]

22. A revision of North American Omphralidae (Scenopinidae) [part]. *Journal of the Kansas Entomological Society* **17**(1): 31–40. [17 March 1944]

23. A revision of North American Omphralidae (Scenopinidae) [concl.]. *Journal of the Kansas Entomological Society* **17**(2): 41–51. [12 June 1944]

24. A new *Pseudotrichia* from Brazil (Omphralidae-Scenopinidae). *Journal of the Kansas Entomological Society* **17**(3): 104–105. [8 July 1944]

1945

20. New Asilidae and Mydaidae (Diptera) in the Snow Collection. *Canadian Entomologist* **76**(11)[1944]: 226–230. [19 January 1945]

25. Revision of Nearctic Bibionidae, including Neotropical *Plecia* and *Penthetria* (Diptera). *Kansas University Science Bulletin* **30**(2): 367–547. [15 June 1945]

1946

27. A new pest of strawberries in Iowa. *Transactions of the Iowa State Horticultural Society* **81**: 165–170. [after 14 November 1946]

1947

26. Nomenclature notes on the family Dorilaidae (Pipunculidae-Diptera). *Journal of the Kansas Entomological Society* **19**(4)[1946]: 135–137. [7 January 1947]

28. The Nearctic *Ptiolina* (Rhagionidae—Diptera) (Rhagionidae—Diptera). *Journal of the Kansas Entomological Society* **20**(1): 1–15. [Co-authored: DEH & **McGuire, J.U**.] [17 February 1947]

29. The genus *Leptopteromyia* (Asilidae-Diptera). *Journal of the Kansas Entomological Society* **20**(2): 72–75. [7 May 1947]

30. Notes and descriptions of Dorilaidae (Pipunculidae-Diptera). *Journal of the Kansas Entomological Society* **20**(4): 146–153. [27 December 1947]

1948

33. *Aristotelia fragariae* Busck on strawberries in Iowa. *Journal of Economic Entomology* **41**(1): 108. [February 1948]

32. Homonymy notes in the Bibionidae. *Journal of the Kansas Entomological Society* **21**(1): 36. [17 March 1948]

37. Neotropical Dorilaidae studies. Part I. *Psyche* **55**(1): 1–15. [30 June 1948]

34. Notes and descriptions of Dorilaidae. Part II. (Pipunculidae–Diptera). *Journal of the Kan-*

sas Entomological Society **21**(3): 88–91. [31 August 1948]

38. Bibionidae-Diptera. *The British Museum (Natural History) Ruwenzori Expedition, 1934–1935* **1**(6): 109–127. [23 October 1948]

35. New and little known Neotropical Dorilaidae. *Journal of the Kansas Entomological Society* **21**(4): 124–133. [30 December 1948]

1949

36. New and little known Diptera in the California Academy of Sciences Collection. *Wasmann Collector* **7**(4)[1948]: 129–137. [18 January 1949]
[Printed date is "December 1948; howver, the issue is stamped as "18 January 1949".]

31. The periodical cicada, brood III, in Iowa. *Proceedings of the Iowa Academy of Science* **54** [1947]: 311–315. [January 1949]
[Dated from the editor's report in vol. 56: 29.]

[ ] [Notes and exhibitions.] New host of melon fly. *Proceedings of the Hawaiian Entomological Society* **13**(3): 339. [25 March 1949]

39. The North American *Chrysopilus* (Rhagionidae—Diptera). *American Midland Naturalist* 41(2): 143–167. [31 March 1949]

40. Studies in Oriental Bibionidae. Part I. *Notes d'Entomologique Chinoise* **13**(1): 1–10. [15 April 1949]

41. New Bibionidae from Madagascar. *Journal of the Kansas Entomological Society* **22**(3): 94–96. [1 July 1949]

42. Studies in Hawaiian fruit flies (Diptera, Tephritidae). *Proceedings of the Entomological Society of Washington* **51**(5): 181–205. [19 October 1949]

43. The African Dorilaidae (Pipunculidae-Diptera). *Mémoires de la Institute Royal des Sciences Naturelles de Belgique* (2) **36**: 1–80. [31 December 1949]

44. New Dorilaidae from the Belgian Congo. *Bulletin de la Institute Royal des Sciences Naturelles de Belgique* **25**(39): 1–10. [December 1949]

1950

[ ] [Notes and exhibitions.] *Lasioderma serricorne* (F.). *Proceedings of the Hawaiian Entomological Society* **14**(1): 6. [30 March 1950]

[ ] [Notes and exhibitions.] *Scholastes palmyra* Curran. *Proceedings of the Hawaiian Entomological Society* **14**(1): 6. [30 March 1950]

[ ] [Notes and exhibitions.] *Eutreta xanthochaeta* Aldrich. *Proceedings of the Hawaiian Entomological Society* **14**(1): 8. [30 March 1950]

[ ] [Notes and exhibitions.] *Aonidiella inornata* McKenzie. *Proceedings of the Hawaiian Entomological Society* **14**(1): 8. [30 March 1950]

[ ] [Notes and exhibitions.] *Euxesta semifasciata* Malloch. *Proceedings of the Hawaiian Entomological Society* **14**(1): 9. [30 March 1950]

[ ] [Notes and exhibitions.] *Scatopse fuscipes* Meigen. *Proceedings of the Hawaiian Entomological Society* **14**(1): 13. [30 March 1950]

[ ] [Notes and exhibitions.] Bethylid in infested books. *Proceedings of the Hawaiian Entomological Society* **14**(1): 18. [30 March 1950]

[ ] [Notes and exhibitions.] *Diarthronomyia chrysanthemi* Ahlberg. *Proceedings of the Hawaiian Entomological Society* **14**(1): 19. [30 March 1950]

[ ] [Notes and exhibitions.] Toxic reaction to a spider bite. *Proceedings of the Hawaiian Entomological Society* **14**(1): 19. [30 March 1950]

45. *Homoneura* vs. *Sciomyza* in Hawaii (Diptera). *Proceedings of the Hawaiian Entomological Society* **14**(1): 73. [30 March 1950]

46. Studies in Pacific Bibionidae (Diptera). Part I. *Proceedings of the Hawaiian Entomological Society* **14**(1): 75–85. [30 March 1950]

47. A new *Dacus* from Australia (Diptera: Tephritidae). *Proceedings of the Hawaiian Entomological Society* **14**(1): 87–89. [30 March 1950]

50. The Nearctic *Nomoneura* and *Nemomydas* (Diptera: Mydaidae). *Wasmann Journal of Biology* **8**(1): 9–37. [17 May 1950]

[Dated from *Wasmann Journal of Biology* 8(3): 382.]

48. Bibionidae (Diptera-Nematocera). *Exploration du Parc National Albert, Mission G.F. de Witte (1933–35)* **65**, 21 p. [14 July 1950]

[Dated from stamped receipt at BMNH.]

49. Dorilaidae, Diptera. *Exploration du Parc National Albert, Mission G.F. de Witte (1933–35)* **62**, 51 p. [2 October 1950]

[Dated from stamped receipt at BMNH.]

51. A monographic study of the African Bibionidae (Diptera). Part I: Introduction and genus *Bibio* Geoffroy. *Journal of the Kansas Entomological Society* **23**(4): 137–153. [9 October 1950]

52. Neotropical Dorilaidae studies. Part II. (Pipunculidae-Diptera). *Revista Entomologica* **21**(3): 433–448. [30 December 1950]

1951

[ ] [Notes and exhibitions.] New spider records. *Proceedings of the Hawaiian Entomological Society* **14**(2): 207. [2 March 1951]

[ ] [Notes and exhibitions.] Calliphorid flies in wool. *Proceedings of the Hawaiian Entomological Society* **14**(2): 208. [2 March 1951]

[ ] [Notes and exhibitions.] *Brontispa chalybeipennis* (Zacher). *Proceedings of the Hawaiian Entomological Society* **14**(2): 208. [2 March 1951]

[ ] [Notes and exhibitions.] Parasites of beet webworm. *Proceedings of the Hawaiian Entomological Society* **14**(2): 208. [2 March 1951]

[ ] [Notes and exhibitions.] A case of apparent human myiasis. *Proceedings of the Hawaiian Entomological Society* **14**(2): 212. [2 March 1951]

[ ] [Notes and exhibitions.] *Argiope appensa* Walckenaer. *Proceedings of the Hawaiian Entomological Society* **14**(2): 214. [2 March 1951]

[ ] [Notes and exhibitions.] *Latrodectus geometricus* Koch. *Proceedings of the Hawaiian Entomological Society* **14**(2): 214. [2 March 1951]

[ ] [Notes and exhibitions.] *Dacus (Strumeta) laticaudus* Hardy. *Proceedings of the Hawaiian Entomological Society* **14**(2): 218. [2 March 1951]

[ ] [Notes and exhibitions.] *Agromyza simplex* Loew. *Proceedings of the Hawaiian Entomological Society* **14**(2): 227. [2 March 1951]

54. Studies in Pacific Bibionidae (Diptera). Part II: Genus *Philia* Meigen. *Proceedings of the Hawaiian Entomological Society* **14**(2): 257–275. [2 March 1951]

55. The Krauss Collection of Australian fruit flies (Tephritidae–Diptera). *Pacific Science* **5**(2): 115–189. [3 May 1951]

57. Proposal that the name “*Dorilas*” Meigen, 1800, should be retained and the name “*Pipunculus*” Latreille [1802–1803] (Class Insecta, Order Diptera) should be treated as a synonym. *Bulletin of Zoological Nomenclature* **2**(2): 144–145. [4 May 1951]

58. Proposed addition to the “Official List of Generic Names in Zoology” of the generic name “*Philia*” Meigen, 1800 (Class Insecta, Order Diptera). *Bulletin of Zoological Nomenclature* **2**(2): 153–154. [4 May 1951]

56. A monographic study of the African Bibionidae (Diptera). Part II: Genus *Philia* Meigen. *Journal of the Kansas Entomological Society* **24**(3): 74–94. [15 June 1951]

53. The Bibionidae (Diptera) of Madagascar. — Part II. *Mémoires de l’Institut Scientifique de Madagascar* (Série A) **5**(2): 323–331. [June 1951]

1952

61. A monographic study of the African Bibionidae (Diptera). Part III: Genus *Plecia. Journal of the Kansas Entomological Society* **25**(1/2): 72–91. [10 February 1952]

[ ] [Notes and exhibitions.] *Phidippus audax* Hentz. *Proceedings of the Hawaiian Entomological Society* **14**(3): 345. [12 March 1952]

[ ] [Notes and exhibitions.] *Chiracanthium* sp. *Proceedings of the Hawaiian Entomological Society* **14**(3): 345. [12 March 1952]

[ ] [Notes and exhibitions.] *Argiope appensa* Walckenaer. *Proceedings of the Hawaiian Entomological Society* **14**(3): 346. [12 March 1952]

[ ] [Notes and exhibitions.] Scale insects on *Araucaria*. *Proceedings of the Hawaiian Entomological Society* **14**(3): 346. [12 March 1952]

[ ] [Notes and exhibitions.] *Homoneura unguiculata* (Kertész). *Proceedings of the Hawaiian Entomological Society* **14**(3): 346. [12 March 1952]

[ ] [Notes and exhibitions.] *Scaptomyza graminum* Fallén. *Proceedings of the Hawaiian Entomological Society* **14**(3): 346. [12 March 1952]

[ ] [Notes and exhibitions.] *Atherigona hendersoni* Malloch. *Proceedings of the Hawaiian Entomological Society* **14**(3): 346. [12 March 1952]

[ ] [Notes and exhibitions.] New spider records. *Proceedings of the Hawaiian Entomological Society* **14**(3): 352. [12 March 1952]

[ ] [Notes and exhibitions.] *Chiracanthium* sp. *Proceedings of the Hawaiian Entomological Society* **14**(3): 352. [12 March 1952]

[ ] [Notes and exhibitions.] *Aphaniosoma* sp. *Proceedings of the Hawaiian Entomological Society* **14**(3): 355. [12 March 1952]

[ ] [Notes and exhibitions.] Notes on Phoridae. *Proceedings of the Hawaiian Entomological Society* **14**(3): 355. [12 March 1952]

[ ] [Notes and exhibitions.] *Lamprolonchaea aurea* (Macquart). *Proceedings of the Hawaiian Entomological Society* **14**(3): 363. [12 March 1952]

[ ] [Notes and exhibitions.] *Ischiodon penicillatus* (Hull). *Proceedings of the Hawaiian Entomological Society* **14**(3): 363. [12 March 1952]

[ ] [Notes and exhibitions.] Corrections [to my paper on the “Krauss Collection of Australian fruit flies”]. *Proceedings of the Hawaiian Entomological Society* **14**(3): 365. [12 March 1952]

[ ] [Notes and exhibitions.] *Latrodectus geometricus* Koch. *Proceedings of the Hawaiian Entomological Society* **14**(3): 369. [12 March 1952]

59. Flies collected in bait traps. *Proceedings of the Hawaiian Entomological Society* **14**(3): 407–409. [12 March 1952]

60. Additions and corrections to Bryan’s check list of the Hawaiian Diptera. *Proceedings of the Hawaiian Entomological Society* **14**(3): 443–484-D. [12 March 1952]

63. Bibionidae and Dorilaidae in the collection of the Musée du Congo Belge. *Revue Zoologique et Botanique Africaine* **46**(1/2): 159–167. [22 August 1952]

[The volume number “44” that appears on reprints and in the corner of the first page of the article is a typographical error. The actual volume number is 46.]

64. Dipteren von den Kleinen Sunda-Inseln aus der Ausbeute der Sunda-Expedition Rensch. V. Bibionidae. *Beiträge zur Entomologie* **2**(4/5): 425–434. [October 1952]

62. Bibionidae et Dorilaidae (Diptera). *Exploration du Parc National de l’Upemba. I. Mission G.F. de Witte (1947–1949)* **8**(5): 57–71. [19 November 1950

[Dated from stamped receipt at BMNH.]

65. Contribution a l’étude des diptères de l’Urundi. III. — Bibionidae et Dorilaidae. *Bulletin de l’Institut Royal des Sciences Naturelles de Belgique* **28**(55): 1–20. [November 1952]

1953

[ ] [Notes and exhibitions.] Two new sepsid flies. *Proceedings of the Hawaiian Entomological Society* **15**(1): 7. [27 March 1953]

[ ] [Notes and exhibitions.] *Cheiracanthium* sp. *Proceedings of the Hawaiian Entomological Society* **15**(1): 18. [27 March 1953]

[ ] [Notes and exhibitions.] New name for carrot aphis. *Proceedings of the Hawaiian Entomological Society* **15**(1): 18. [27 March 1953]

66. New Hawaiian Tipulidae (Diptera). *Proceedings of the Hawaiian Entomological Society* **15**(1): 55–58. [27 March 1953]

67. Studies in Hawaiian Dorilaidae (Diptera). Part I. *Proceedings of the Hawaiian Entomological Society* **15**(1): 59–73. [27 March 1953]

68. Notes on the Shannon types of Dorilaidae from Argentina (Pipunculidae-Diptera). *Acta Zoologica Lilloana* **10**[1952]: 299–306. [March 1953]
[Date stamped on reprint.]

69. The Argentine «Bibionidae» (Diptera). *Acta Zoologica Lilloana* **12**[1951]: 343–376. [March 1953]
[Date stamped on reprint.]

71. The Bibionidae of New Zealand (Diptera). *Pacific Science* **8**(2): 147–204. [7 October 1953]

70. Studies in Oriental Bibionidae: new species of *Plecia* and *Penthetria* and a revision of the *Plecia impostor* complex. (Bibionidae: Diptera). *Records of the Indian Museum* **50**(1): 89–104. [22 December 1953]
[From colophon date.]

1954

73. The *Dacus* subgenera *Neodacus* and *Gymnodacus* of the world (Diptera, Tephritidae). *Proceedings of the Entomological Society of Washington* **56**(1): 5–23. [26 February 1954]

[ ] [Notes and exhibitions.] *Tenodera australasiae* (Leach). *Proceedings of the Hawaiian Entomological Society* **15**(2): 278. [5 March 1954]

[ ] [Notes and exhibitions.] Nitidulidae spp. *Proceedings of the Hawaiian Entomological Society* **15**(2): 278. [5 March 1954]

[ ] [Notes and exhibitions.] *Neoexaireta spinigera* (Wiedemann). *Proceedings of the Hawaiian Entomological Society* **15**(2): 278. [5 March 1954]

[ ] [Notes and exhibitions.] *Anthomyia bisetosa* Thomson. *Proceedings of the Hawaiian Entomological Society* **15**(2): 278. [5 March 1954]

[ ] [Notes and exhibitions.] Unidentified woody galls. *Proceedings of the Hawaiian Entomological Society* **15**(2): 290. [5 March 1954]

[ ] [Notes and exhibitions.] *Prosthetochaeta fasciata* Grimshaw. *Proceedings of the Hawaiian Entomological Society* **15**(2): 290. [5 March 1954]

72. Notes and descriptions of Australian fruit flies (Diptera: Tephritidae). *Proceedings of the Hawaiian Entomological Society* **15**(2): 327–333. [5 March 1954]

74. Studies in the fruit flies of the Philippine Islands, Indonesia, and Malaya. Part I. Dacini (Tephritidae–Diptera). *Pacific Science* **8**(2): 147–204. [Co-authored: DEH & **Adachi, M.S**.] [30 April 1954]

77. Records of Bibionidae in the Musée Royal du Congo Belge, Tervuren. *Annales du Musée du Congo Belge* [4° Serie] (Zoologie) **1**: 378–380. [June 1954]

75. Studies in New World Dorilaidae (Pipunculidae–Diptera). *Journal of the Kansas Entomological Society* **27**(4): 121–127. [27 October 1954]

76. Neotropical Dorilaidae studies, Part III. Brazilian species and a key to the known species of *Dorilas sens. lat. Boletin do Museu Nacional* (Zoología) **123**: 1–60. [17 September 1954]

1955

78. *Sphaeniscus* Becker and *Euphranta* Loew of the Oriental and Pacific regions (Tephritidae-Diptera). *Pacific Science* **9**(1): 77–84. [January 1955]

79. The *Dacus* (*Afrodacus*) Bezzi of the world (Tephritidae, Diptera*). Journal of the Kansas Entomological Society* **28**(1): 3–15. [25 January 1955]

80. Contributions a l'étude de la faune entomologique du Ruanda-Urundi (Mission P. Basilewsky 1953). XXVIII. Diptera, Bibionidae and Dorilaidae. *Annales du Musée du Congo Belge* [8° Serie] (Zoologie) **36**: 283–286. [March 1955]

[ ] [Notes and exhibitions.] *Cheiracanthium diversum* Koch. *Proceedings of the Hawaiian Entomological Society* **15**(3): 374. [20 June 1955]

1956

81. A reclassification of the Dacini (Tephritidae-Diptera). *Annals of the Entomological Society of America* **48**(6): 425–437. [12 January 1956]

82. Diptera: Dorilaidae (Pipunculidae). *Insects of Micronesia* **13**(1): 1–9. [14 February 1956]

83. Diptera: Tephritidae. *Insects of Micronesia* **14**(1): 1–28. [Co-authored: DEH & **Adachi, M.S**.] [17 February 1956]

[ ] [Notes and exhibitions.] *Aphis fabae* Scopoli. *Proceedings of the Hawaiian Entomological Society* **16**(1): 5. [16 July 1956]

[ ] [Notes and exhibitions.] *Nysius nigriscutellatus* Usinger. *Proceedings of the Hawaiian Entomological Society* **16**(1): 6. [16 July 1956]

[ ] [Notes and exhibitions.] *Centruroides gracilis* (Latreille). *Proceedings of the Hawaiian Entomological Society* **16**(1): 6. [16 July 1956]

[ ] [Notes and exhibitions.] *Melanagromyza splendida* Frick. *Proceedings of the Hawaiian Entomological Society* **16**(1): 9. [16 July 1956]

[ ] [Notes and exhibitions.] *Ceratoxys latiuscula* (Loew). *Proceedings of the Hawaiian Entomological Society* **16**(1): 11. [16 July 1956]

[ ] [Notes and exhibitions.] *Araecerus levipennis* Jordan. *Proceedings of the Hawaiian Entomological Society* **16**(1): 11. [16 July 1956]

[ ] [Notes and exhibitions.] *Oestrus ovis* (L.). *Proceedings of the Hawaiian Entomological Society* **16**(1): 13–14. [16 July 1956]

[ ] [Notes and exhibitions.] *Dettopsomyia nigrovittata* (Malloch). *Proceedings of the Hawaiian Entomological Society* **16**(1): 17. [16 July 1956]

85. New Hawaiian Sciaridae (Diptera). *Proceedings of the Hawaiian Entomological Society* **16**(1): 72–90. [16 July 1956]

86. Date of publication of volume 8, number 1, of the *Queensland Journal of Agricultural Science*. *Proceedings of the Hawaiian Entomological Society* **16**(1): 70–71. [16 July 1956]

84. The Walker types of Bibionidae (Diptera). *Journal of the Kansas Entomological Society* **29**(3): 85–91. [31 July 1956]

87. Proposed acceptance of "*Lestodiplosis*" as the valid original spelling for the generic name spelled both in this way and as "*Leptodiplosis*" by Kieffer in 1894 (Class Insecta, Order Diptera). *Bulletin of Zoological Nomenclature* **12**(6): 176–177. [24 August 1956]

88. Proposed use of the plenary powers to validate the generic name "*Campsicnemus*" Haliday, 1851 (Class Insecta, Order Diptera). *Bulletin of Zoological Nomenclature* **12**(6): 178–180. [24 August 1956]

89. Dorilaidae (Pipunculidae) from the Commonwealth Institute of Entomology. *Proceedings of the Royal Entomological Society of London* (B) **25**(9/10): 180–182. [19 October 1956]

1957

91. Diptera: Bibionidae and Scatopsidae. *Insects of Micronesia* **12**(2): 87–102. [20 January 1957]

90. Diptera: Coelopidae. *Insects of Micronesia* **14**(2): 41–46. [21 January 1957]

93. New Neotropical Bibionidae in the Naturhistorisches Museum, Vienna. *Annalen des Naturhistorisches Museum in Wien* **61**: 238–240. [April 1957]

[ ] [Notes and exhibitions.] *Gasteracantha cancriformis* (L.). *Proceedings of the Hawaiian Entomological Society* **16**(2): 187. [13 May 1957]

[ ] [Notes and exhibitions.] *Cheiracanthium diversum* Koch. *Proceedings of the Hawaiian Entomological Society* **16**(2): 187. [13 May 1957]

[ ] [Notes and exhibitions.] *Phytobia maculosa* (Malloch). *Proceedings of the Hawaiian Entomological Society* **16**(2): 188. [13 May 1957]

[ ] [Notes and exhibitions.] *Mycophila fungicola* Felt. *Proceedings of the Hawaiian Entomological Society* **16**(2): 189. [13 May 1957]

[ ] [Notes and exhibitions.] *Arthrocnodax walkeriana* Felt. *Proceedings of the Hawaiian Entomological Society* **16**(2): 189. [13 May 1957]

[ ] [Notes and exhibitions.] *Lestremia cinerea* Macquart; *Lestremia leucophaea* (Meigen). *Proceedings of the Hawaiian Entomological Society* **16**(2): 189. [13 May 1957]

[ ] [Notes and exhibitions.] *Anachaetopsis tortricis* (Coquillett). *Proceedings of the Hawaiian Entomological Society* **16**(2): 195. [13 May 1957]

[ ] [Notes and exhibitions.] *Macrosiphum granarum* (Kirby). *Proceedings of the Hawaiian Entomological Society* **16**(2): 197. [13 May 1957]

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[ ] [Notes and exhibitions.] Destruction of collections at the Hungarian National Museum. *Proceedings of the Hawaiian Entomological Society* **16**(3): 320. [Co-authored: **Gressitt, J.L**. & DEH] [21 July 1958]

[ ] [Notes and exhibitions.] *Corythucha morrilli* Osborn and Drake. *Proceedings of the Hawaiian Entomological Society* **16**(3): 321–322. [21 July 1958]

[ ] [Notes and exhibitions.] *Phytobia (Amauromyza) maculosa* (Malloch). *Proceedings of the Hawaiian Entomological Society* **16**(3): 323. [21 July 1958]

[ ] [Notes and exhibitions.] Insects on alfalfa, *Medicago sativa* L. *Proceedings of the Hawaiian Entomological Society* **16**(3): 323. [21 July 1958]

[ ] [Notes and exhibitions.] Theraphosid spider. *Proceedings of the Hawaiian Entomological Society* **16**(3): 336. [21 July 1958]

95. A review of the genera *Sophira* Walker and *Tritaeniopteron* De Meijere (Diptera: Tephritidae). *Proceedings of the Hawaiian Entomological Society* **16**(3): 366–378. [21 July 1958]

98. Family Bibionidae. *In*: Guide to the insects of Connecticut. Part VI. The Diptera or true flies of Connecticut. Sixth fascicle: March flies and gall-midges. *Bulletin of the Connecticut State Geological and Natural History Survey* **87**: 5–46. [23 September 1958]

[Dated from library receipt at SI.]

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97. Diptera: Omphralidae (Scenopinidae). *Insects of Micronesia* **13**(2): 11–13. [24 October 1958]

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99. Obituary notice for Dr. Martin L. Aczél, 1906–1958. *Proceedings of the Entomological Society of Washington* **61**(3): 139–140. [29 June 1959]

100. Dorilaidae (Diptera Cyclorrhapha) addendum. *Exploration du Parc National Albert, Mission G.F. de Witte (1933–35)* **95**(2): 27–29. [25 July 1959]

[ ] [Notes and exhibitions.] *Toxorhynchites splendens* (Wiedemann). *Proceedings of the Hawaiian Entomological Society* **17**(1): 6. [31 August 1959]

[ ] [Notes and exhibitions.] Changes in names of Hawaiian Sarcophagidae. *Proceedings of the Hawaiian Entomological Society* **17**(1): 27. [31 August 1959]

[ ] [Notes and exhibitions.] *Scadra* sp. *Proceedings of the Hawaiian Entomological Society* **17**(1): 27. [31 August 1959]

[ ] [Notes and exhibitions.] *Macrosiphum pisi* (Harris). *Proceedings of the Hawaiian Entomological Society* **17**(1): 28. [31 August 1959]

101. A review of the genus *Pseudiastata* Coquillett (Drosophilidae, Diptera). *Proceedings of the Hawaiian Entomological Society* **17**(1): 76–82. [31 August 1959]

102. Proposed use of the plenary powers to suppress the generic names *Prothecus* Rondani, 1856, and *Alloneura* Rondani, 1856, for the purpose of validating the generic names *Verrallia* Mik, 1899, and *Tomosvaryella* Aczél, 1939 (Class Insecta, Order Diptera). *Bulletin of Zoological Nomenclature* **17**(1/2): 27–29. [10 October 1959]

104. The Walker types of fruit flies (Tephritidae-Diptera) in the British Museum collection. *Bulletin of the British Museum (Natural History)* (Entomology) **8**(5): 159–242. [November 1959]

105. A new Bibionidae from California (Diptera). *Pan-Pacific Entomologist* **35**(4): 209–211. [8 December 1959]

1960

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108. Diptera: Nematocera — Brachycera (except Dolichopodidae). *Insects of Hawaii* 10, vii + 368 p. [31 March 1960]
[Dated from information supplied by the publisher.]

109. *Paracacoxenus*, new genus, with notes on *Cacoxenus indagator* Loew (Diptera: Drosophilidae). *Annals of the Entomological Society of America* **53**(3): 356–359. [Co-authored: DEH & **Wheeler, M.**] [31 May 1960]

106. Catalog of the Neotropical Bibionidae (Diptera, Nematocera). *Acta Zoologica Lilloana* **17**[1959]: 437–476. [10 June 1960]

[ ] [Notes and exhibitions.] *Drosophila bizonata* Kikkawa and Peng. *Proceedings of the Hawaiian Entomological Society* **17**(2): 163. [2 August 1960]

[ ] [Notes and exhibitions.] A stylopised fruit fly. *Proceedings of the Hawaiian Entomological Society* **17**(2): 163. [2 August 1960]

[ ] [Notes and exhibitions.] *Macrosiphum ibarae* Matsumura. *Proceedings of the Hawaiian Entomological Society* **17**(2): 163. [2 August 1960]

[ ] [Notes and exhibitions.] *Gasteracantha cancriformis* (L.). *Proceedings of the Hawaiian Entomological Society* **17**(2): 166. [2 August 1960]

[ ] [Notes and exhibitions.] *Melanagromyza splendida* Frick. *Proceedings of the Hawaiian Entomological Society* **17**(2): 168. [2 August 1960]

[ ] [Notes and exhibitions.] *Orthezia insignis* Browne. *Proceedings of the Hawaiian Entomological Society* **17**(2): 168. [2 August 1960]

[ ] [Notes and exhibitions.] *Macrosiphum pisi* (Harris). *Proceedings of the Hawaiian Entomological Society* **17**(2): 168. [2 August 1960]

[ ] [Notes and exhibitions.] *Hypoderma bovis* (L.). *Proceedings of the Hawaiian Entomological Society* **17**(2): 169. [2 August 1960]

[ ] [Notes and exhibitions.] *Cryptophlebia illepida* (Butler). *Proceedings of the Hawaiian Entomological Society* **17**(2): 169. [2 August 1960]

[ ] [Notes and exhibitions.] New Hawaiian *Scaptomyza*. *Proceedings of the Hawaiian Entomological Society* **17**(2): 171–172. [2 August 1960]

[ ] [Notes and exhibitions.] *Homoneura striatifrons* (de Meijere). *Proceedings of the Hawaiian Entomological Society* **17**(2): 174. [2 August 1960]

[ ] [Notes and exhibitions.] *Macrosiphum pisi* (Harris). *Proceedings of the Hawaiian Entomological Society* **17**(2): 174. [2 August 1960]

[ ] [Notes and exhibitions.] *Grassiella* sp. *Proceedings of the Hawaiian Entomological Society* **17**(2): 180. [2 August 1960]

110. A new *Bibio* from the Sierra Mountains, California, and a new *Plecia* from Malaya (Diptera: Bibionidae). *Proceedings of the Hawaiian Entomological Society* **17**(2): 255–259. [2 August 1960]

112. An unusual new Nematocera from Japan (Diptera), and a new family name. *Pacific Insects* **2**(3): 263–267. [Co-authored: DEH & **Nagatomi, A**.] [10 October 1960]

111. Revision of the Japanese Bibionidae (Diptera, Nematocera). *Pacific Insects* **2**(4): 383–449. [Co-authored: DEH & **Takahashi, M**.] [20 December 1960]

1961

113. Diptera (Nematocera): Bibionidae. *South African Animal Life* **7**[1960]: 210–215. [2 May 1961]

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114. Notes and descriptions of exotic Bibionidae. *Proceedings of the Entomological Society of Washington* **63**(2): 81–99. [20 June 1961]

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[Given out on the first day of the Congress, which was held from 21 August to 7 September 1961.]

[ ] [Notes and exhibitions.] *Corythuca morrilli* Osborn and Drake. *Proceedings of the Hawaiian Entomological Society* **17**(3): 313. [30 August 1961]

[ ] [Notes and exhibitions.] Hawaiian Lepidoptera names. *Proceedings of the Hawaiian Entomological Society* **17**(3): 318. [30 August 1961]

[ ] [Notes and exhibitions.] Human myiasis. *Proceedings of the Hawaiian Entomological Society* **17**(3): 319. [30 August 1961]

115. Bibionidae (Diptera Nematocera) and Dorilaidae (Pipunculidae: Diptera-Cyclorrhapha). *Exploration du Parc National Garamba, Mission H. de Saeger* **24**(3): 111–180 [31 October 1961]

116. The Bibionidae of California. *Bulletin of the California Insect Survey* **6**(7): 179–195. [23 December 1961]

117. The Diptera of Hawaii. *Verhandlungen der XI. Internationaler Kongress für Entomologie* (Wien) **1**: 167–168. [December 1961]

[Dated from Coulson, J.R. *et al*., 1965, *U.S. Department of Agriculture, Agriculture Handbook*. 276: 1245.]

1962

118. New insect pests in Hawaii. *Hawaii Farm Science* **11**(2): 6–9. [April 1962]

119. The Bibionidae (Diptera) of Madagascar part III. *Verhandlungen der Naturforschende Gesellschaft in Basel* **73**(1): 149–170. [20 July 1962]

120. Notes and descriptions of Pipunculidae from the Natal Museum, South Africa. *Annals of the Natal Museum* **15**(2): 255–266. [August 1962]

[ ] [Notes and exhibitions.] *Scadra rufidens* Stål. *Proceedings of the Hawaiian Entomological Society* **18**(1): 16. [24 August 1962]

[ ] [Notes and exhibitions.] *Chiracanthium diversum* Koch. *Proceedings of the Hawaiian Entomological Society* **18**(1): 16. [24 August 1962]

124. Studies in Pipunculidae of Colombia. *Proceedings of the Hawaiian Entomological Society* **18**(1): 259–266. [24 August 1962]

123. A remarkable new bibionid fly from Australia (Diptera: Bibionidae). *Pacific Insects* **4**(4): 783–785. [15 December 1962]

121. Insects of Macquarie Island. Diptera: Coelopidae. *Pacific Insects* **4**(4): 963–971. [15 December 1962]

122. Preliminary studies of Pipunculidae of Madagascar (Diptera). *Verhandlungen der Naturforschende Gesellschaft in Basel* **73**(2): 241–269. [31 December 1962]

1963

[ ] [Notes and exhibitions.] Brown spots on anthuriums. *Proceedings of the Hawaiian Entomological Society* **18**(2): 195–196. [29 July 1963]

[ ] [Notes and exhibitions.] *Nezara viridula smaragdula* (Fabricius). *Proceedings of the Hawaiian Entomological Society* **18**(2): 196. [29 July 1963]

[ ] [Notes and exhibitions.] *Volucella tamaulipana* Townsend. *Proceedings of the Hawaiian Entomological Society* **18**(2): 201. [29 July 1963]

[ ] [Notes and exhibitions.] *Nezara viridula smaragdula* (Fabricius). *Proceedings of the Hawaiian Entomological Society* **18**(2): 201. [29 July 1963]

[ ] [Notes and exhibitions.] *Oligotoma (Aposthonia) oceania* Ross. *Proceedings of the Hawaiian Entomological Society* **18**(2): 203. [29 July 1963]

[ ] [Notes and exhibitions.] *Scadra rufidens* Stål. *Proceedings of the Hawaiian Entomological Society* **18**(2): 208. [29 July 1963]

[ ] [Notes and exhibitions.] *Hippelates collusor* (Townsend). *Proceedings of the Hawaiian Entomological Society* **18**(2): 210–211. [29 July 1963]

1964

126. A re-study of Perkins types of Australian Pipunculidae (Diptera) and the type of *Pipunculus vitiensis* Muir from Fiji. *Australian Journal of Zoology* **12**(1): 84–125. [April 1964]

125. Diptera: Brachycera, family Dolichopodidae. Cyclorrhapha, series Aschiza. Families Lonchopteridae, Phoridae, Pipunculidae, and Syrphidae. *Insects of Hawaii* **11**, vii + 458 p. [30 April 1964]
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125. Dolichopodidae. *Insects of Hawaii* **11**: 12–296. [Co-authored: DEH & **Kohn, M.A**.] [30 April 1964]
[Dated from information supplied by the publisher.]

125. Phoridae. *Insects of Hawaii* **11**: 262–302. [Co-authored: DEH & **Beyer, E.M.**] [30 April 1964]
[Dated from information supplied by the publisher.]

[ ] [Notes and exhibitions.] *Trupanea* n. sp. *Proceedings of the Hawaiian Entomological Society* **18**(3): 330. [30 June 1964]

[ ] [Notes and exhibitions.] *Tefflus zanzibaricus alluaudi* Sternberg. *Proceedings of the Hawaiian Entomological Society* **18**(3): 337. [30 June 1964]

[ ] [Notes and exhibitions.] *Mezira membranacea* (Fabricius). *Proceedings of the Hawaiian Entomological Society* **18**(3): 338. [30 June 1964]

[ ] [Notes and exhibitions.] *Ambylomma cyprium cyprium* Neumann. *Proceedings of the Hawaiian Entomological Society* **18**(3): 345. [30 June 1964]

127. Diptera from Nepal. The fruit flies (Diptera, Tephritidae). *Bulletin of the British Museum (Natural History)* (Entomology) **15**(6): 154–169. [27 July 1964]

1965

128. The Pipunculidae of Argentina. *Acta Zoologica Lilloana* **19**[1963]: 187–241. [January 1965]

[Dated from stamped date on reprint.]

129. Diptera from Nepal. Bibionidae. *Bulletin of the British Museum (Natural History)* (Entomology) **16**(1): 3–23. [3 June 1965]

[ ] [Notes and exhibitions.] *Mumetopia nigrimana* (Coquillett). *Proceedings of the Hawaiian Entomological Society* **19**(1): 7. [25 June 1965]

[ ] [Notes and exhibitions.] *Donaceus nigronotatus* Cresson. *Proceedings of the Hawaiian Entomological Society* **19**(1): 19. [25 June 1965]

[ ] [Notes and exhibitions.] *Telmatogeton abnormis* (Terry). *Proceedings of the Hawaiian Entomological Society* **19**(1): 19. [25 June 1965]

[ ] [Notes and exhibitions.] *Oscinella* sp. *Proceedings of the Hawaiian Entomological Society* **19**(1): 19. [25 June 1965]

[ ] [Notes and exhibitions.] Predation on native *Drosophila* larvae. *Proceedings of the Hawaiian Entomological Society* **19**(1): 34. [25 June 1965]

130. Neotropical Pipunculidae (Diptera) studies, part IV. Further studies of Brasilian species. *Arquivos de Zoologia* **14**(1): 1–67. [25 July 1965]

131. Diptera: Cyclorrhapha II. Series Schizophora section Acalypteratae. I. Family Drosophilidae. *Insects of Hawaii* **12**, vii + 814 p. [31 August 1965]

[Dated from information supplied by the publisher.]

133. Family Bibionidae, p. 191–196. *In*: Stone, A., C.W. Sabrosky, W.W. Wirth, R.H. Foote & J.R. Coulson (eds.), A catalog of the Diptera of America north of Mexico. *U.S. Department of Agriculture, Agriculture Handbook* **276**, iv + 1696 p. [23 August 1965]

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133. Family Scenopinidae, p. 354–356. *In*: Stone, A., C.W. Sabrosky, W.W. Wirth, R.H. Foote & J.R. Coulson, (eds.), A catalog of the Diptera of America north of Mexico. *U.S. Department of Agriculture, Agriculture Handbook* **276**, iv + 1696 p. [23 August 1965]

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133. Family Pipunculidae, p. 550–557. *In*: Stone, A., C.W. Sabrosky, W.W. Wirth, R.H. Foote & J.R. Coulson, (eds.), A catalog of the Diptera of America north of Mexico. *U.S. Department of Agriculture, Agriculture Handbook* **276**, iv + 1696 p. [23 August 1965]

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132. Evolution and genetics of Hawaiian Drosophilidae. *Proceedings of the XII International Congress of Entomology* (London) **1965**: 119. [31 December 1965+]

1966

134. Redescriptions of Brunetti's species of *Bibio* from India (Diptera-Bibionidae). *Annals and Magazine of Natural History* (13) **8**[1965]: 201–217. [20 January 1966]

135. Diptera from Nepal. Pipunculidae (Dorilaidae). *Bulletin of the British Museum (Natural History)* (Entomology) **17**(10): 439–449. [15 March 1966]

136. Family Bibionidae. *Catalog of the Diptera of the Americas South of the United States* **18**: 1–20. [20 May 1966]

137. Family Pipunculidae. *Catalog of the Diptera of the Americas South of the United States* **45**: 1–15. [20 May 1966]

138. Family Scenopinidae. *Catalog of the Diptera of the Americas South of the United States* **32**: 1–5. [20 May 1966]

139. The Walker types of fruit flies (Diptera: Tephritidae) in the British Museum. Part III. *Journal of the Kansas Entomological Society* **39**(4): 658–668. [2 December 1966]

1967

140. Redescription of *Tomosvaryella frontata* (Becker) (Diptera: Pipunculidae). *Annals of the Entomological Society of America* **60**(1): 116–118. [16 January 1967]

[ ] [Notes and exhibitions.] *Culex pipiens quinquefasciatus* Say. *Proceedings of the Hawaiian Entomological Society* **19**(2)[1966]: 123. [31 January 1967]

[ ] [Notes and exhibitions.] *Phorocantha semipunctata* Fabricius, new to the state. *Proceedings of the Hawaiian Entomological Society* **19**(2)[1966]: 123. [31 January 1967]

[ ] [Notes and exhibitions.] *Conicera (Tritoconicera) hawaiiensis* Colyer (Phoridae) a new record for island of Hawaii. *Proceedings of the Hawaiian Entomological Society* **19**(2)[1966]: 128. [31 January 1967]

[ ] [Notes and exhibitions.] *Culex pipiens quinquefasciatus* Say. *Proceedings of the Hawaiian Entomological Society* **19**(2)[1966]: 139. [31 January 1967]

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[The printed year of publication has "1 August 1966", but a handwritten note by the author on a reprint states that the actual publication date was "February 1967".]

142. The Bibionidae (Diptera) of Nepal, results of the Austrian and the B.P. Bishop Museum Expeditions, 1961 and 1965. *Pacific Insects* **9**(3): 519–536. [22 August 1967]

143. 109. Bibionidae. Ergebnisse der zoologischen Forschungen von Dr. Z. Kaszab in der Mongolei (Diptera). *Reichenbachia* **9**(22): 191–200. [20 September 1967]

145. The types of Bibionidae (Diptera) in the Naturhistorisches Museum, Wien. *Annalen des Naturhistorisches Museum in Wien* **70**: 169–181. [October 1967]

144. Studies of fruitflies associated with mistletoe in Australia and Pakistan with notes and descriptions on genera related to *Perilampsis* Bezzi. Diptera: Tephritidae. *Beiträge zur Entomologie* **17**(1/2): 127–149. [29 December 1967]
[Date received at the library of the Museum für Naturkunde, Humboldt-Universität, Berlin (M. Ohl, pers. comm.).]

1968

[ ] [Notes and exhibitions.] *Loewimyia*, n. sp. *Proceedings of the Hawaiian Entomological Society* **19**(3)[1967]: 323. [13 March 1968]

[ ] [Notes and exhibitions.] *Loewimyia* n. sp. *Proceedings of the Hawaiian Entomological Society* **19**(3)[1967]: 326. [13 March 1968]

[ ] [Notes and exhibitions.] *Bryania bipunctata* Aldrich. *Proceedings of the Hawaiian Entomological Society* **19**(3)[1967]: 326. [13 March 1968]

[ ] [Notes and exhibitions.] *Acinia picturata* (Snow) (Diptera: Tephritidae). *Proceedings of the Hawaiian Entomological Society* **19**(3)[1967]: 326. [13 March 1968]

[ ] [Notes and exhibitions.] *Oscinella formosa* Becker (Diptera: Chloropidae). *Proceedings of the Hawaiian Entomological Society* **19**(3)[1967]: 326. [13 March 1968]

[ ] [Notes and exhibitions.] *Paroxyna sororcula* (Wiedemann), [1830, Ausseureur. Sweifl. Ins. 2: 509. (Tephritidae: Diptera)]. *Proceedings of the Hawaiian Entomological Society* **19**(3)[1967]: 333. [13 March 1968]

146. New picture-winged *Drosophila* from Hawaii. *University of Texas Publications* **6818**: 171–262 [Co-authored: DEH & **Kaneshiro, K.Y**.] [15 September 1968]

148. Bibionidae and Pipunculidae of the Philippines and Bismarck Islands (Diptera). *Entomologiske Meddelelser* **36**: 417–507. [20 November 1968]
[= Noona Dan Papers No. 67.]

147. Bibionidae (Diptera) of New Guinea. *Pacific Insects* **10**(3/4): 443–513. [25 December 1968]

149. The fruit fly types in the Naturhistorisches Museum, Wien (Tephritidae-Diptera). *Annalen des Naturhistorisches Museum in Wien* **72**: 107–155. [November 1968]

1969

150. The Bibionidae (Diptera) of the Philippines. *Pacific Insects* **11**(1): 117–154. [Co-authored: DEH & **Delfinado, M.D**.] [4 March 1969]
[The printed publication date is 20 February 1969, but the actual publication is 4 March 1969 based on information from the publisher.]

[ ] [Notes and exhibitions.] *Euxesta quadrivittata* (Macq.) and *Euxesta wettsteini* Hendel. *Proceedings of the Hawaiian Entomological Society* **20**(1)[1968]: 323. [11 March 1969]

152. IV. Descriptions of new Hawaiian *Drosophila*. *University of Texas Publication* **6918**: 39–54. [Co-authored: DEH & **Kaneshiro, K.Y**.] [15 September 1969]

153. VI. Notes on Hawaiian "*idiomyia*" (*Drosophila*). *University of Texas Publication* **6918**: 71–77. [15 September 1969]

151. Lectotype designations for fruit flies (Diptera: Tephritidae). *Pacific Insects* **11**(2): 477–481. [6 October 1969]
[The printed publication date is 30 August 1969, but the actual publication is 6 October 1969 based on information from the publisher.]

1970

[ ] [Notes and exhibitions.] *Culex pipiens quinquefasciatus* Say. *Proceedings of the Hawaiian Entomological Society* **20**(2)[1969]: 323. [4 February 1970]

154. Taxonomy and distribution of the Oriental fruit fly and related species (Tephritidae-Diptera). *Proceedings of the Hawaiian Entomological Society* **20**(2)[1969]: 395–428. [4 February 1970]

155. Myiasis of new-born calves in Hawaii. *Proceedings of the Hawaiian Entomological Society* 20(2)[1969]: 435–438. [Co-authored: **Shishido, W.H**. & DEH] [4 February 1970]

156. [Note.] Die Lonchaeidae und Pallopteridae Österreichs und der angrezenden Gebeite. II: Die Pallopteridae by G. Morge. *Entomological News* **80**(12)[1969]: 322. [20 February 1970]
[Dated from the January 1970 issue.]

158. Tephritidae (Diptera) collected by the Noona Dan Expedition in the Philippines and Bismarck Islands [part]. *Entomologiske Meddelelser* **38**(1): 71–96. [15 June 1970]
[= Noona Dan Papers No. 95.]

157. The evolutionary biology of the Hawaiian Drosophilidae, p. 437–543. *In*: Hecht, M.K. & W.C. Steere (eds.), *Essays in evolution and genetics in honor of Theodosius Dobzhansky, a supplement to Evolutionary Biology*. Appleton-Century-Crofts, New York. xv + 594 p. [Co-authored: **Carson, H.L**., DEH, **Speith, H.T**. and **Stone, W.S**.] [June 1970]
[Dated from information supplied by the publisher.]

158. Tephritidae (Diptera) collected by the Noona Dan Expedition in the Philippines and Bismarck Islands [concl.]. *Entomologiske Meddelelser* **38**(2): 97–136. [30 September 1970]
[= Noona Dan Papers No. 95.]

1971

[ ] [Notes and exhibitions.] *Goeldichironomus holoprasinus* (Goeldi). *Proceedings of the Hawaiian Entomological Society* **20**(3)[1970]: 487–488. [28 January 1971]

[ ] [Notes and exhibitions.] *Iridomyrmex humilis* (Mayr). *Proceedings of the Hawaiian Entomological Society* **20**(3)[1970]: 488. [28 January 1971]

[ ] [Notes and exhibitions.] *Sepedon sauteri* Hendel. *Proceedings of the Hawaiian Entomological Society* **20**(3)[1970]: 502. [28 January 1971]

[ ] [Notes and exhibitions.] *Lonchaea polita* Say and *L. striatifrons* Malloch. *Proceedings of the Hawaiian Entomological Society* **20**(3)[1970]: 502. [28 January 1971]

[ ] [Notes and exhibitions.] *Lamprolonchaea metatarsata* Kertész. *Proceedings of the Hawaiian Entomological Society* **20**(3)[1970]: 502–503. [28 January 1971]

159. VII. New picture-winged *Drosophila* from Hawaii, part II. (Drosophilidae, Diptera). *University of Texas Publication*s **7103**: 151–170. [Co-authored: DEH & **Kaneshiro, K.Y**.] [1 February 1971]

160. Type specimens of Philippine Diptera. *Notulae Entomologicae* **51**: 15–32. [Co-authored: **Delfinado, M.D.** & DEH] [31 March 1971]

161. A new *Plecia* (Diptera: Bibionidae) from Mexican amber. *University of California Publications in Entomology* **63**: 65–67. [16 July 1971]

162. Diptera: Bibionidae from Ceylon. *Entomologica Scandinavica Supplement* **1**: 286. [10 November 1971]

163. Diptera: Tephritidae from Ceylon. *Entomologica Scandinavica Supplement* **1**: 287–292. [10 November 1971]

165. Evolution of the Hawaiian Drosophilidae (Insecta: Diptera), p. 147–148. *In*: *Symposium on Indian Ocean and Adjacent Seas, their origin, science and resources*. Cochin, India, 1971. Marine Biological Association of India, Cochin. [31 December 1971+]

1972

[ ] [Notes and exhibitions.] *Phormia regina* (Meigen). *Proceedings of the Hawaiian Entomological Society* **21**(1)[1971]: 2. [February 1972]

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1991

[ ] [Notes and exhibitions.] *Nephrotoma suturalis wulpiana* (Bergroth) (Diptera: Tipulidae). *Proceedings of the Hawaiian Entomological Society* **30**: 2–3. [18 February 1991]

[ ] [Notes & exhibitions.] New tipulid on Oahu. *Hawaiian Entomological Society Newsletter* 1(2): 2. [20 June 1991]

231. Book review: Fauna of New Zealand. Bibionidae (Insecta: Diptera). Number 20. By Roy Harrison. 25 pp. *Annals of the Entomological Society of America* **84**(5): 568–69. [September]

230. Contribution of taxonomic studies to the integrated pest management of fruit flies with emphasis on the Asia-Pacific region, p. 44–48. *In*: Vijaysegaran, S. & A.G. Ibrahim (eds.), *Fruit flies in the tropics. Proceedings of the First International Symposium, 14-16 March 1988, Kuala Lumpur, Malaysia.* Malaysian Agricultural Research and Development Institute (MARDI) & Malaysian Plant Protection Society, Kuala Lumpur. vii + 430 p. [31 December 1991+]

1992

[ ] [Notes & exhibitions.] Diptera new to the Hawaiian Islands. *Hawaiian Entomological Society Newsletter* **2**(1): 2. [March 1992]

[ ] [Notes & exhibitions.] New snail parasitoid in Hawaii. *Hawaiian Entomological Society Newsletter* **2**(2): 3. [June 1992]

1993

232. Book review: Fruit flies of economic significance. Their identification and bionomics. By I.M. White & M. Elson-Harris. 601 pp. *Environmental Entomology* **22**(1): 1408. [February 1993]

[ ] [Notes and exhibitions.] Nomenclatural changes for Pacific Tephritidae (Diptera). *Proceedings of the Hawaiian Entomological Society* **31**[1992]: 1–2. [15 March 1993]

[ ] [Notes and exhibitions.] *Taeniaptera angulata* (Loew) (Diptera: Micropezidae). *Proceedings of the Hawaiian Entomological Society* **31**[1992]: 5. [15 March 1993]

[ ] [Notes and exhibitions.] Names changes for Hawaiian Diptera. *Proceedings of the Hawaiian Entomological Society* 31[1992]: 8. [15 March 1993]

[ ] [Notes & exhibitions.] New records of Diptera for Hawaii. *Hawaiian Entomological Society Newsletter* **3**(1): 2. [27 August 1993]

1995

[ ] [Notes and exhibitions.] *Trentepohlia (Mongoma) australasiae* (Diptera: Tipulidae). *Proceedings of the Hawaiian Entomological Society* **32**: 2. [10 August 1995]

[ ] [Notes and exhibitions.] New records of Diptera for the Hawaiian Islands. *Proceedings of the Hawaiian Entomological Society* **32**: 5–6. [10 August 1995]

[ ] [Notes and exhibitions.] *Johnsonia elegans* Coquillett (Diptera: Sarcophagidae). *Proceedings of the Hawaiian Entomological Society* **32**: 6. [10 August 1995]

[ ] [Notes and exhibitions.] *Hippelates proboscideus* Williston (Diptera: Chloropidae). *Proceedings of the Hawaiian Entomological Society* **32**: 8. [10 August 1995]

[ ] [Notes and exhibitions.] *Poecilominettia sexseriata* Hendel (Diptera: Lauxaniidae). *Proceedings of the Hawaiian Entomological Society* **32**: 8. [10 August 1995]

1996

233. Revision of the Australian Tephritini (Diptera: Tephritidae). *Invertebrate Taxonomy* **10**(2): 213–405. [Co-Authored: DEH & **Drew, R.A.I**.] [4 April 1996]

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234. Review of the *haleakalae* species group of Hawaiian *Drosophila* (Diptera: Drosophilidae). *Bishop Museum Bulletin in Entomology* **9**, viii + 88 p. [Co-authored: DEH, **Kaneshiro, K.Y**., **Val, F.C**. & **O'Grady, P.M**.] [10 October 2001]

[Dated from information supplied by the publisher. Authorship of new species in this paper is "Hardy & Kaneshiro".]

235. The *rustica* species group of Hawaiian *Drosophila* (Diptera: Drosophilidae). *Pan-Pacific Entomologist* **77**(4): 254–260. [Co-authored: **O'Grady, P.M**., **Val, F.C**. DEH & **Kaneshiro, K.Y**.] [7 December 2001]

[Authorship of new species in this paper is "Hardy & Kaneshiro".]

Undated

[ ] Errata [to Hardy, 1943, *Kansas University Science Bulletin* **29**(1): 1-231.] [Unnumbered page]

[No date or source for this errata is currently known. But based on Hardy's position title at the University of Hawaii in the credit line and the format and style it is presumed that it dates from between 1948 and 1951 and that it was issued by the *Kansas University Science Bulletin*.]

List of Taxa described by D. Elmo Hardy (1936–2001)

The following lists all the new taxa proposed by Hardy as well as replacement names he proposed. For each name, the name (original genus and epithet for species), author, year and page is given, and, if the status of the name has changed, the valid name or epithet is given in brackets at the end.

FAMILY-GROUP NAMES -- total 3

Canthyloscelididae -1
Hyperoscelidae Hardy & Nagatomi, 1960: 263 [= Canthyloscelididae]

Pipunculidae -1
Tomosvaryellinae Hardy, 1943: 25

Xenasteiidae -1
Xenasteiidae Hardy, 1980: 205

GENUS-GROUP NAMES -- total 107

Asilidae -1
Bromleyus Hardy, 1944: 226

Bibionidae -3
Enicoscolus Hardy, 1961: 81
Heteroplecia Hardy, 1950: 75 [= Plecia, subgenus]
Pleciodes Hardy, 1952: 76 [= Plecia, subgenus]

Canthyloscelididae -1
Hyperoscelis Hardy & Nagatomi, 1960: 263

Cecidomyiidae -1
Heterocontarinia Hardy, 1960: 271

Drosophilidae -8
Antopocerus Hardy, 1965: 42 [= Drosophila]
Ateledrosophila Hardy, 1965: 62 [= Drosophila]
Celidosoma Hardy, 1965: 66
Exalloscaptomyza Hardy, 1965: 604 [= Scaptomyza, subgenus]
Grimshawomyia Hardy, 1965: 535
Nudidrosophila Hardy, 1965: 564 [= Drosophila]
Paracacoxenus Hardy, 1960: 358
Trichotobregma Hardy, 1965: 532 [= Drosophila]

Keroplatidae -1
Trigemma Hardy, 1960: 201

Mydidae -1
Heteromydas Hardy, 1944: 227

Pipunculidae -3
Allomethus Hardy, 1943: 128
Congomyia Hardy, 1949: 7
Wittella Hardy, 1950: 41 [= Cephalops]

Pyrgotidae -1
Austromyia Hardy, 1954: 327 [= Neotoxura]

Scenopinidae -1
Belosta Hardy, 1944: 37
Brevitrichia Hardy, 1944: 32

Tephritidae -78
Acinoeuphranta Hardy, 1971: 288
Aciuropsis Hardy, 1974: 96
Adramoides Hardy, 1973: 128
Alincocallistomyia Hardy, 1986: 28
Alloeomyia Hardy, 1986: 29
Anchiacanthonevra Hardy, 1986: 31
Antisophira Hardy, 1974: 103
Brandtomyia Hardy, 1987: 68
Buloloa Hardy, 1986: 32
Collessomyia Hardy & Drew, 1996: 231
Cooronga Hardy & Drew, 1996: 233
Craspedoxanthitea Hardy, 1987: 285
Crinitisophira Hardy, 1987: 69
Curticella Hardy, 1959: 209
Curvinervus Hardy, 1959: 203 [= Stymbara]
Dietheria Hardy, 1973: 183
Ectopomyia Hardy, 1973: 101
Elleipsa Hardy, 1970: 90 [= Plestometopon]
Emheringia Hardy, 1989: 512
Epacrocerus Hardy, 1982: 79
Exallosophira Hardy, 1980: 149
Freyomyia Hardy, 1974: 67
Galbifascia Hardy, 1973: 247
Gressittidium Hardy, 1986: 64
Griphomyia Hardy, 1987: 290
Hemiclusiosoma Hardy, 1986: 66
Hemigymnodacus Hardy, 1973: 19 [= Bactrocera (Paratridacus)]
Hemizeugodacus Hardy, 1951: 131 [= Bactrocera, subgenus]
Hendelina Hardy, 1951: 179
Heringomyia Hardy, 1968: 131
Heringomyia Hardy, 1986: 67 [= Emheringia]
Heterodaculus Hardy, 1951: 134 [= Bactrocera, subgenus]
Heterosophira Hardy, 1973: 130 [= Sophira]
Homiothemara Hardy, 1988: 101
Hyalopeza Hardy & Drew, 1996: 253
Hyponeothemara Hardy, 1986: 71 [= Hexaresta]
Ichneumonopsis Hardy, 1973: 132
Javadacus Hardy, 1983: 26
Lalokia Hardy, 1987: 309
Liepana Hardy & Drew, 1996: 256
Mimoeuphranta Hardy, 1986: 79
Mimosophira Hardy, 1973: 106
Nothoclusiosoma Hardy, 1986: 85
Othniocera Hardy, 1986: 87
Paedohexacinia Hardy, 1986: 92
Paraactinoptera Hardy & Drew, 1996: 299
Paracanthonevra Hardy, 1974: 73
Paraceratitella Hardy, 1967: 138
Paraclusiosoma Hardy, 1986: 52 [= Clusiosoma, subgenus]
Paracristobalia Hardy, 1987: 345
Paraeuphranta Hardy, 1959: 173
Parahyalopeza Hardy & Drew, 1996: 303
Paraphasca Hardy, 1986: 94
Pararhabdochaeta Hardy, 1985: 61
Parasophira Hardy, 1980: 145
Paraspathulina Hardy & Drew, 1996: 304
Paraxarnuta Hardy, 1973: 195

Peneparoxyna Hardy & Drew, 1996: 315
Polyaroidea Hardy, 1988: 105
Proepacrocerus Hardy, 1988: 110
Pseudoneothemara Hardy, 1986: 111
Quasicooronga Hardy & Drew, 1996: 328
Quasirhabdochaeta Hardy, 1986: 114
Rabauliomorpha Hardy, 1970: 122
Rhaibophleps Hardy, 1973: 203
Robertsomyia Hardy, 1983: 228
Saucromyia Hardy, 1986: 125
Scolocolus Hardy, 1970: 95
Sophiropsis Hardy, 1986: 126
Spaniothrix Hardy, 1973: 206 [= Sophira (Kambangania)]
Stigmatomyia Hardy, 1986: 129
Tanaodema Hardy, 1987: 350
Tanymetopus Hardy, 1982: 88
Tarphobregma Hardy, 1987: 353
Tetrameringophrys Hardy, 1973: 165 [= Dimeringophrys]
Udamolobium Hardy, 1982: 90
Walkeraitia Hardy, 1986: 177
Xenosophira Hardy, 1980: 157

Therevidae -1
Zionea Hardy, 1938: 144 [= Nebritus]

Xenasteiidae -1
Xenasteia Hardy, 1980: 211

SPECIES-GROUP NAMES -- total 1867

Asilidae - 7
Bromleyus flavidorsus Hardy, 1944: 226
Erax cuervanus Hardy, 1943: 27 [= Efferia]
Leptogaster bifidus Hardy, 1942: 59 [= Beameromyia]
Leptogaster occidentis Hardy, 1942: 61 [= Beameromyia]
Leptopteromyia americana Hardy, 1947: 74
Nicocles bromleyi Hardy, 1943: 28
Stenopogon huachucanus Hardy, 1942: 57

Asteiidae - 7
Asteia aberrans Hardy & Delfinado, 1980: 233
Asteia mauiensis Hardy & Delfinado, 1980: 238
Asteia molokaiensis Hardy & Delfinado, 1980: 238
Asteia montgomeryi Hardy & Delfinado, 1980: 239
Asteia palikuensis Hardy & Delfinado, 1980: 242
Asteia sabroskyi Hardy & Delfinado, 1980: 244
Loewimyia orbiculata Hardy, 1980: 249

Bibionidae - 305
Bibio ablusus Hardy, 1965: 9
Bibio adjunctus Hardy & Takahashi, 1960: 407
Bibio affiniproximus Hardy, 1965: 10
Bibio ainoi Hardy & Takahashi, 1960: 408
Bibio amputonervis Hardy & Takahashi, 1960: 409
Bibio aneuretus Hardy & Takahashi, 1960: 411
Bibio anposis Hardy, 1968: 444
Bibio aquilus Hardy, 1967: 528
Bibio araeoceles Hardy, 1967: 529
Bibio beameri Hardy, 1945: 451
Bibio bisepta Hardy, 1937: 204 [= melanopilus]
Bibio brevicruris Hardy, 1950: 145
Bibio brunetti Hardy, 1973: 435
Bibio carolinus Hardy, 1945: 457
Bibio cognatus Hardy, 1937: 199
Bibio columbiaensis Hardy, 1938: 207
Bibio conjunctivus Hardy, 1937: 200 [= albipennis]
Bibio conus Hardy, 1938: 208 [= striatipes]
Bibio currani Hardy, 1937: 200 [= nigritus]
Bibio dacunhai Hardy, 1981: 151
Bibio deceptus Hardy & Takahashi, 1960: 413
Bibio flavihalter Hardy & Takahashi, 1960: 415
Bibio fluginatus Hardy, 1937: 201
Bibio flukei Hardy, 1937: 202
Bibio gilvus Hardy, 1937: 206 [= nigrifemoratus]
Bibio gracilipalpis Hardy & Takahashi, 1960: 417
Bibio hennigi Hardy, 1952: 425
Bibio holomaurus Hardy & Takahashi, 1960: 419
Bibio illaudatus Hardy, 1961: 94
Bibio imparilis Hardy, 1959: 209
Bibio jacobi Hardy, 1938: 209 [= rufitibialis]
Bibio kenyaensis Hardy, 1950: 148
Bibio knowltoni Hardy, 1937: 202
Bibio lobatus Hardy, 1937: 203
Bibio lucens Hardy, 1937: 203 [= nigripilus]
Bibio medianus Hardy & Takahashi, 1960: 423
Bibio melanopilosus Hardy, 1936: 195
Bibio metaclavipes Hardy & Takahashi, 1960: 425
Bibio mickeli Hardy, 1937: 204
Bibio montanus Hardy & Takahashi, 1960: 426
Bibio necotus Hardy, 1937: 205
Bibio neojacobi Hardy, 1945: 476 [= rufitibialis]
Bibio nepalensis Hardy, 1967: 532
Bibio nigriclavipes Hardy & Takahashi, 1960: 428
Bibio nigrifemoratus Hardy, 1937: 206
Bibio obuncus Hardy & Takahashi, 1960: 429
Bibio omani Hardy & Takahashi, 1960: 431
Bibio paltidus Hardy, 1937: 203 [= knowltoni]
Bibio pruinosus Hardy, 1950: 151
Bibio rufalipes Hardy, 1937: 207
Bibio rufitibialis Hardy, 1938: 209
Bibio ryukyuensis Hardy & Takahashi, 1960: 436
Bibio scaurus Hardy, 1965: 16
Bibio sericatus Hardy, 1937: 207
Bibio sierrae Hardy, 1960: 255
Bibio signatus Hardy, 1937: 208 [= xanthopus]
Bibio simulans Hardy & Takahashi, 1960: 438
Bibio singularis Hardy & Takahashi, 1960: 439
Bibio stonei Hardy, 1942: 142 [= vicinus]
Bibio teneus Hardy, 1937: 208
Bibio totonigrum Hardy, 1965: 18
Bibio townesi Hardy, 1945: 487
Bibio upembensis Hardy, 1952: 58
Bibio utahensis Hardy, 1937: 208
Bibio velcidus Hardy, 1937: 209
Bibio wulpi Hardy, 1953: 349
Bibio xuthopteron Hardy, 1968: 450
Bibionellus aczeli Hardy, 1953: 345
Dilophus aberratus Hardy, 1982: 822
Dilophus aquilonia Hardy & Takahashi, 1960: 443
Dilophus atelestes Hardy, 1937: 210 [= tibialis]
Dilophus atripennis Hardy, 1982: 824
Dilophus beckeri Hardy, 1948: 36
Dilophus brevirostrum Hardy & Takahashi, 1960: 445
Dilophus cantrelli Hardy, 1982: 825
Dilophus collessi Hardy, 1982: 826
Dilophus conformis Hardy, 1968: 456
Dilophus conspicuus Hardy, 1982: 828
Dilophus crenulatus Hardy & Delfinado, 1969: 148
Dilophus dichromatus Hardy, 1968: 457
Dilophus discretus Hardy, 1982: 830
Dilophus dubius Hardy, 1982: 831

Dilophus flavicrus Hardy, 1982: 831
Dilophus fulviventris Hardy & Takahashi, 1960: 446
Dilophus gracilis Hardy, 1968: 421
Dilophus harrisoni Hardy, 1953: 515
Dilophus hirsutus Hardy, 1965: 22
Dilophus innubilus Hardy & Delfinado, 1969: 149
Dilophus longipilosus Hardy, 1982: 833
Dilophus mcalpinei Hardy, 1982: 836
Dilophus modicus Hardy, 1982: 837
Dilophus partitus Hardy, 1982: 839
Dilophus parvus Hardy, 1982: 839
Dilophus paucidens Hardy, 1962: 170
Dilophus pictilis Hardy & Delfinado, 1969: 150
Dilophus sexspinosus Hardy, 1982: 844
Dilophus skusei Hardy, 1982: 845
Dilophus surrufus Hardy, 1982: 847
Dilophus tersus Hardy, 1982: 848
Dilophus tetrascolus Hardy, 1982: 850
Dilophus transvestis Hardy, 1968: 463
Dilophus tricuspidatus Hardy, 1982: 851
Dilophus variceps Hardy, 1942: 133
Enicoscolus brachycephalus Hardy, 1961: 82
Enicoscolus collessi Hardy, 1962: 783
Enicoscolus dolichocephalus Hardy, 1961: 82
Penthetria appendicula Hardy, 1945: 384
Penthetria brunetti Hardy, 1948: 36
Penthetria distincta Hardy, 1945: 385
Penthetria formosana Hardy, 1953: 103
Philia anomalus Hardy, 1942: 127 [= Dilophus]
Philia arizonaensis Hardy, 1937: 209 [= Dilophus]
Philia bakeri Hardy, 1951: 260 [= Dilophus]
Philia brazilensis Hardy, 1948: 36 [= Dilophus]
Philia buxtoni Hardy, 1948: 123 [= Dilophus]
Philia crinitus Hardy, 1951: 262 [= Dilophus]
Philia edwardsi Hardy, 1948: 36 [= Dilophus]
Philia exiguus Hardy, 1951: 263 [= Dilophus]
Philia globosus Hardy, 1942: 128[= Dilophus]
Philia golbachi Hardy, 1953: 364 [= Dilophus]
Philia inconnexus Hardy, 1961: 94 [= Dilophus]
Philia jamesi Hardy, 1937: 210 [= Dilophus obesulus]
Philia lucidus Hardy, 1948: 125 [= Dilophus]
Philia minimus Hardy, 1942: 129 [= Dilophus]
Philia multispinosus Hardy, 1951: 266 [= Dilophus]
Philia niger Hardy, 1937: 212 [= Dilophus]
Philia obsoletus Hardy, 1951: 91 [= Dilophus]
Philia oklahomensis Hardy, 1937: 211 [= Dilophus occipitalis]
Philia ornatus Hardy, 1942: 130 [= Dilophus]
Philia peruensis Hardy, 1948: 36 [= Dilophus]
Philia philippii Hardy, 1959: 470 [= Dilophus]
Philia quadridens Hardy, 1953: 370 [= Dilophus]
Philia quinquespinae Hardy, 1961: 96 [= Dilophus]
Philia quintanus Hardy, 1951: 270 [= Dilophus]
Philia rostrata Hardy, 1951: 271 [= Dilophus longirostris]
Philia sayi Hardy, 1959: 471 [= Dilophus]
Philia segregatus Hardy, 1961: 98 [= Dilophus]
Philia serenus Hardy, 1953: 371 [= Dilophus]
Philia splendens Hardy, 1951: 92
Philia tingi Hardy, 1942: 132
Philia tuthilli Hardy, 1953: 518
Philia vicarius Hardy, 1948: 127
Plecia acuminata Hardy, 1968: 470
Plecia adiastola Hardy & Takahashi, 1960: 395
Plecia affinidecora Hardy, 1968: 470
Plecia affiniparva Hardy & Delfinado, 1969: 122
Plecia aliena Hardy, 1948: 109
Plecia americana Hardy, 1940: 15
Plecia amplitergum Hardy, 1967: 522
Plecia nigra spp. argentina Hardy, 1953: 353 [= full species]
Plecia assamensis Hardy, 1949: 1
Plecia avicephaliforma Hardy, 1940: 16
Plecia basalis Hardy, 1948: 110
Plecia bequaerti Hardy, 1952: 160
Plecia biarmata Hardy, 1942: 105
Plecia bidens Hardy, 1948: 111
Plecia bifida Hardy, 1968: 474
Plecia biformis Hardy, 1942: 106
Plecia bilobata Hardy, 1948: 113
Plecia bisulca Hardy, 1968: 474
Plecia brachystylata Hardy & Delfinado, 1969: 125
Plecia brazilana Hardy, 1942: 106
Plecia burmensis Hardy, 1958: 193
Plecia cana Hardy, 1950: 76
Plecia capitata Hardy, 1951: 324
Plecia celodens Hardy, 1962: 152
Plecia chinensis Hardy, 1949: 2
Plecia rufithorax spp. concava Hardy, 1942: 114 [= full species]
Plecia connata Hardy, 1962: 153
Plecia coronata Hardy, 1951: 326
Plecia crenula Hardy, 1968: 478
Plecia curta Hardy, 1948: 114
Plecia curtispina Hardy, 1968: 481
Plecia curvistylata Hardy, 1942: 107
Plecia cuspidata Hardy, 1968: 481
Plecia decepta Hardy, 1953: 91
Plecia decora Hardy, 1950: 78
Plecia dentata Hardy, 1942: 107
Plecia diopsa Hardy & Delfinado, 1969: 127
Plecia disjuncta Hardy, 1958: 195
Plecia disparis Hardy, 1942: 108
Plecia dispersa Hardy, 1958: 196
Plecia diversa Hardy, 1958: 202
Plecia duplicis Hardy, 1968: 486
Plecia ecuadorensis Hardy, 1942: 108
Plecia edwardsi Hardy, 1940: 17
Plecia elongata Hardy, 1952: 79
Plecia erebeoidea Hardy, 1982: 814
Plecia evexa Hardy, 1962: 154
Plecia exechia Hardy & Delfinado, 1969: 128
Plecia flavibasis Hardy, 1962: 156
Plecia freemani Hardy, 1962:
Plecia furva Hardy, 1952: 429
Plecia fuscinervis Hardy, 1948: 115
Plecia gibbosa Hardy, 1942: 109
Plecia gilvipennis Hardy, 1949: 94
Plecia gressitti Hardy, 1953: 92
Plecia gurneyi Hardy, 1950: 79
Plecia hadrosoma Hardy & Takahashi, 1960: 397
Plecia hamata Hardy, 1968: 489
Plecia impensa Hardy, 1957: 238
Plecia impilosa Hardy, 1940: 17
Plecia inconspicua Hardy, 1950: 79
Plecia incurvata Hardy, 1942: 110
Plecia insolita Hardy, 1952: 82
Plecia intercedens Hardy, 1953: 95
Plecia intricata Hardy, 1968: 491
Plecia jubata Hardy & Delfinado, 1969: 131
Plecia keiseri Hardy, 1962: 151
Plecia laffooni Hardy, 1950: 80
Plecia lateodens Hardy, 1962: 157
Plecia lateralis Hardy, 1940: 18
Plecia laticlavum Hardy, 1962: 159
Plecia lieftincki Hardy, 1968: 493

Plecia longipalpus Hardy, 1962: 160
Plecia lopesi Hardy, 1940: 19
Plecia maculata Hardy, 1942: 110
Plecia madagascarensis Hardy, 1949: 95
Plecia magnispina Hardy, 1958: 206
Plecia malabarana Hardy, 1949: 4
Plecia malayaensis Hardy, 1948: 36
Plecia malkini Hardy, 1952: 83
Plecia mallochi Hardy, 1948: 36
Plecia manni Hardy, 1950: 82
Plecia mayoensis Hardy, 1950: 84
Plecia membranifera Hardy & Takahashi, 1960: 398
Plecia mexicana Hardy, 1937: 199 [= Penthetria]
Plecia ecuadorensis spp. micans Hardy, 1942: 108 [= full species]
Plecia monticola Hardy, 1958: 209
Plecia multilobata Hardy, 1968: 495
Plecia nagatomii Hardy & Takahashi, 1960: 399
Plecia nearctica Hardy, 1940: 20
Plecia neglecta Hardy, 1953: 97
Plecia nilgirensis Hardy, 1949: 5
Plecia obtusicornis Hardy, 1968: 496
Plecia obtusilobata Hardy, 1968: 497
Plecia octodentata Hardy, 1948: 117
Plecia oculastra Hardy, 1968: 499
Plecia odontata Hardy, 1962: 162
Plecia okadai Hardy & Takahashi, 1960: 401
Plecia paenerubescens Hardy, 1961: 112
Plecia pagdeni Hardy, 1960: 258
Plecia palauensis Hardy, 1957: 88
Plecia panamaensis Hardy, 1942: 111
Plecia paracollaris Hardy, 1961: 88
Plecia parvistylata Hardy, 1942: 112
Plecia patula Hardy, 1968: 500
Plecia pauliani Hardy, 1951: 329
Plecia perplexa Hardy, 1942: 112
Plecia persimilis Hardy, 1940: 21
Plecia pertinens Hardy, 1942: 112
Plecia peruviana Hardy, 1961: 89
Plecia platystila Hardy, 1957: 239
Plecia platyura Hardy & Delfinado, 1969: 136
Plecia prolixa Hardy, 1962: 164
Plecia propeforcipata Hardy, 1968: 501
Plecia propria Hardy, 1968: 503
Plecia pruinosa Hardy, 1940: 22
Plecia pudica Hardy, 1968: 420
Plecia pullata Hardy, 1949: 7
Plecia pulliparva Hardy & Delfinado, 1969: 138
Plecia punctulata Hardy, 1940: 23
Plecia quadrata Hardy, 1952: 83
Plecia quasimaculata Hardy, 1961: 90
Plecia quatei Hardy, 1967: 524
Plecia recaviterga Hardy & Delfinado, 1969: 138
Plecia reclusa Hardy, 1962: 165
Plecia rectiora Hardy, 1942: 113
Plecia redunca Hardy, 1952: 84
Plecia retusa Hardy, 1962: 166
Plecia rhinigera Hardy, 1968: 504
Plecia robusta Hardy, 1950: 11
Plecia pullata ssp. rubicunda Hardy, 1953: 98 [= pulllata]
Plecia rufimarginata Hardy, 1940: 24
Plecia rufiscutella Hardy, 1940: 24
Plecia rugosa Hardy, 1940: 25
Plecia sana Hardy, 1948: 118
Plecia scenica Hardy, 1952: 86
Plecia septentrionalis Hardy, 1953: 98
Plecia serrata Hardy, 1942: 114
Plecia serrifera Hardy, 1968: 505
Plecia siamensis Hardy, 1953: 100
Plecia sinensis Hardy, 1953: 101
Plecia spilota Hardy, 1968: 506
Plecia stricta Hardy, 1968: 508
Plecia stuckenbergi Hardy, 1962: 167
Plecia sundaensis Hardy, 1952: 432
Plecia tecta Hardy, 1949: 8
Plecia tenebrosa Hardy, 1958: 215
Plecia tetrascolata Hardy, 1968: 509
Plecia thulinigra Hardy, 1961: 93
Plecia tridens Hardy, 1958: 217
Plecia trifida Hardy, 1968: 510
Plecia trilobata Hardy, 1942: 114
Plecia uberta Hardy, 1942: 115
Plecia ugandaensis Hardy, 1948: 119
Plecia uncinata Hardy, 1948: 121
Plecia varabilis Hardy, 1942: 115
Plecia visenda Hardy, 1950: 75
Plecia wittei Hardy, 1950: 7
Plecia xenia Hardy, 1942: 109
Plecia yabaensis Hardy, 1952: 89
Plecia yunnanica Hardy, 1953: 102
Plecia zamboanga Hardy, 1950: 84
Plecia zernyi Hardy, 1952: 89

Calliphoridae - 2
Dyscritomyia alta Hardy, 1981: 303
Dyscritomyia viridis Hardy, 1981: 347

Canacidae - 6
Procanace acuminata Hardy & Delfinado, 1980: 389
Procanace bifurcata Hardy & Delfinado, 1980: 392
Procanace confusa Hardy & Delfinado, 1980: 394
Procanace constricta Hardy & Delfinado, 1980: 396
Procanace quadrisetosa Hardy & Delfinado, 1980: 401
Procanace wirthi Hardy & Delfinado, 1980: 404

Canthyloscelidae - 1
Hyperoscelis insignis Hardy & Nagatomi, 1960: 265 [= eximia]

Carnidae - 3
Aphaniosoma macalpinei Hardy, 1980: 174
Aphaniosoma minutum Hardy, 1980: 174
Gymnochiromyia hawaiiensis Hardy, 1980: 177

Cecidomyiidae - 13
Coccodiplosis ananasae Hardy, 1960: 283
Giardomyia furvescens Hardy, 1960: 287
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Scolocolus bicolor Hardy, 1970: 96
Soita baltazarae Hardy, 1974: 151
Soita ensifera Hardy, 1974: 152
Sophira disjuncta Hardy, 1980: 141 [= ypsilon]
Sophira kurahashii Hardy, 1980: 131
Sophira linduensis Hardy, 1980: 135
Sophira medioflava Hardy, 1974: 83
Sophira philippinensis Hardy, 1974: 84
Sophira spectabilis Hardy, 1980: 139
Sophiropsis calcarata Hardy, 1986: 128
Spaniothrix vittata Hardy, 1973: 206 [= Sophira]
Sphenella novaguineensis Hardy, 1988: 62
Staurocneros imitator Hardy, 1970: 99 [= Coelotrypes circumscriptus]
Stigmatomyia arcuata Hardy, 1986: 129
Stylia apiciclara Hardy, 1973: 326 [= Campiglossa orientalis]
Stylia philippinensis Hardy, 1974: 248 [= Campiglossa]
Stylia siamensis Hardy, 1973: 329 [= Campiglossa]
Stylia spenceri Hardy, 1973: 330 [= Campiglossa]
Tanaodema porrecta Hardy, 1987: 351
Tanymetopus claripennis Hardy, 1982: 88
Tarphobregma carinatifrons Hardy, 1987: 354
Tarphobregma pandani Hardy, 1987: 356
Tephrella heringi Hardy, 1970: 129 [= Hendrella]
Tephrella trimaculata Hardy, 1988: 17 [= Hendrella]
Tephritis brunnea Hardy & Drew, 1996: 352 [= Austrotephritis]
Tephritis bushi Hardy & Drew, 1996: 354 [= Austrotephritis]
Tephritis cardualis Hardy, 1974: 373
Tephritis coei Hardy, 1964: 164 [Campiglossa]
Tephritis daedala Hardy, 1964: 166
Tephritis distigmata Hardy & Drew, 1996: 356 [= Austrotephritis]
Tephritis furcata Hardy & Drew, 1996: 358
Tephritis hesperia Hardy & Drew, 1996: 360 [= Austrotephritis]
Tephritis pantosticta Hardy & Drew, 1996: 362 [= Payahyalopeza]
Tephritis phaeostigma Hardy & Drew, 1996: 367 [= Austrotephritis]
Tephritis prolixa Hardy & Drew, 1996: 371 [= Paraactinoptera]
Tephritis protrusa Hardy & Drew, 1996: 373 [= Austrotephritis]
Tephritis pumila Hardy & Drew, 1996: 376 [= Austrotephritis]
Tephritis quasiprolixa Hardy & Drew, 1996: 378 [= Austrotephritis]
Tephritis tasmaniae Hardy & Drew, 1996: 380 [= Austrotephritis]
Tephritis trupanea Hardy & Drew, 1996: 381 [= Austrotephritis]
Termitorioxa timorensis Hardy, 1986: 132
Tetrameringophrys parilis Hardy, 1973: 165 [= Dimeringophrys pallidipennis]
Themara horsfilldi Hardy, 1977: 69 [= maculipennis]
Themara ostensackeni Hardy, 1974: 91
Themarohystrix alpina Hardy, 1986: 143
Themarohystrix bivittata Hardy, 1986: 145
Themarohystrix hyalina Hardy, 1986: 147
Themarohystrix nigrifacies Hardy, 1986: 149
Themarohystrix perkinsi Hardy, 1986: 149
Themarohystrix variabilis Hardy, 1986: 151
Themaroides robertsi Hardy, 1986: 156
Themaroides vittata Hardy, 1986: 158
Themaroides xanthosoma Hardy, 1986: 160
Themaroidopsis quinquevittata Hardy, 1986: 162
Themaroidopsis rufescens Hardy, 1986: 163
Themaroidopsis tetraspilota Hardy, 1986: 164
Tritaeniopteron elachispilotum Hardy, 1973: 115 [= tetraspilotum]
Tritaeniopteron flavifacies Hardy, 1974: 92
Tritaeniopteron tetraspilotum Hardy, 1973: 115
Trupanea apicalis Hardy, 1980: 64
Trupanea arboreae Hardy, 1980: 66
Trupanea artemisiae Hardy, 1980: 68
Trupanea beardsleyi Hardy, 1980: 69
Trupanea bidensicola Hardy, 1980: 72
Trupanea bifida Hardy & Drew, 1996: 387
Trupanea brunneipennis Hardy, 1973: 333
Trupanea celaenoptera Hardy, 1980: 72
Trupanea decepta Hardy, 1970: 114
Trupanea dempta Hardy, 1980: 78
Trupanea denotata Hardy, 1980: 80
Trupanea heronensis Hardy & Drew, 1996: 390
Trupanea isolata Hardy, 1973: 335
Trupanea joycei Hardy, 1980: 84
Trupanea latinota Hardy, 1988: 74
Trupanea lipochaetae Hardy, 1980: 88
Trupanea lyneborgi Hardy, 1970: 131
Trupanea marginalis Hardy, 1980: 90
Trupanea megaspila Hardy, 1980: 91
Trupanea neoapicalis Hardy, 1989: 530 [= apicalis]

Trupanea nigripennis Hardy, 1980: 92
Trupanea notata Hardy & Drew, 1996: 393
Trupanea pantosticta Hardy, 1980: 93
Trupanea pekeloi Hardy, 1980: 95
Trupanea perkinsi Hardy, 1980: 97
Trupanea prolata Hardy & Drew, 1996: 395
Trupanea pusilla Hardy & Drew, 1996: 397
Trupanea queenslandensis Hardy & Drew, 1996: 398
Trupanea rufa Hardy, 1988: 79
Trupanea simplicissima Hardy & Foote, 1989: 531 [= simplex]
Trupanea terryi Hardy, 1988: 83
Trupanea vernoniae Hardy, 1973: 337
Trypanocentra adjusta Hardy, 1986: 176 [= nigripennis]
Trypanocentra atrifacies Hardy, 1986: 173
Trypanocentra bipectinata Hardy, 1986: 174
Trypanocentra gressitti Hardy, 1986: 176
Trypanocentra longicornis Hardy, 1986: 168
Trypanocentra mallochi Hardy, 1986: 169
Trypanocentra tricuneata Hardy, 1986: 172
Trypeta aberrans Hardy, 1973: 279
Trypeta accola Hardy, 1973: 281 [= Vidalia]
Udamolobium pictulum Hardy, 1982: 90
Vidalia bicolor Hardy, 1987: 364
Vidalia ceratophera Hardy, 1977: 116
Vidalia tuberculata Hardy, 1970: 108
Xanthorrachis assamensis Hardy, 1973: 283
Xanthorrachis sabahensis Hardy, 1988: 119
Xarnuta sabahensis Hardy, 1986: 184
Xarnuta stellaris Hardy, 1970: 85
Xenosophira invibrissata Hardy, 1980: 158
Xenosophira vibrissata Hardy, 1980: 159
Tethinidae - 3
Apetaneus watsoni Hardy, 1962: 965
Dasyrhicnoessa vockerothi Hardy & Delfinado, 1980: 373
Pelomyia steyskali Hardy & Delfinado, 1980: 375

Therevidae - 4
Epomyia flavipes Hardy, 1943: 26 [= Cyclotelus]
Psilocephala squamosa Hardy, 1943: 24 [= Brachylinga]
Thereva utahensis Hardy, 1938: 145
Zionea tanneri Hardy, 1938: 144 [= Nebritus]

Xenasteiidae - 7
Xenasteia aldabrae Hardy, 1980: 215
Xenasteia divergens Hardy, 1980: 216
Xenasteia okinawaensis Hardy, 1980: 217
Xenasteia palauensis Hardy, 1980: 218
Xenasteia sabroskyi Hardy, 1980: 221
Xenasteia seychellensis Hardy, 1980: 222
Xenasteia similis Hardy, 1980: 224

Xylophagidae - 1
Dialysis kesseli Hardy, 1948: 129

Keeping Score

Keeping score is a grand old American tradition: From sports where there are numerous statistics for every game to almost every other activity, Americans have found ways to assess how people perform, at least quantitatively.

In the sciences, counting prizes (like Nobels) to publications and their impact factors (like citation index) are common, but these measures do not really apply well to taxonomists. Years ago, Alexander (1942) suggested ranking taxonomists by the number of species they described. Later quantitative scores to measure a worker's ability to discover and identify species (taxonomy) and their names (nomenclature) were proposed (Thompson & Pedersen, 1986).

None of these measures have been used much as gathering the data has been very difficult. Now with near completion of the biosystematic Database of World Diptera (Thompson, 2003), at least some basic statistics can be easily generated. So, we have ranked Elmo with his peers, historical and contemporaneous, and Elmo stands among the best, the most productivity dipterists of all times.

Our table provides the following items: **Column 1.** The last name of the dipterist; **Column 2.** Year of the birth of the dipterist; **Column 3.** Year of the death of the dipterist; **Column 4.** Number of available names proposed by the dipterist. This includes names now considered as junior synonyms, homonyms, unjustified replacement names and emendations; **Column 5.** Number of species. This is the number of names proposed that are currently considered to represent valid species; **Column 6.** Percentage of names that are considered valid today; **Column 7.** Year of first scientific publication; **Column 8.** Year of last scientific publication; **Column 9.** Average number of species described per working year (column 4 divided by column 12); **Column 10.** Number of major scientific publications. Major being used in the sense of publications that contain critical taxonomic and nomenclatural data, not all the various notes, book reviews and other popular writings. For some authors, we have used their own lists of publications and have taken only those that they themselves have numbered (such Alexander, Hardy, *et alia*). Otherwise we have counted those publications listed in standard bibliographic sources such as Hagen (1862–1863), Horn & Schlenkling (1928–1929); Derksen & Scheiding (1965–1975) and Zoological Record. For some of these authors, the BioSystematic Database of World Diptera is now completed and was therefore used as a source. **Column 11.** Age of author at death; **Column 12.** Number of years worked (column 7 minus column 8); **Column 13.** Average number of publications per working year.

Table 1. Statistics on the top thirteen dipterists.

Author	Birth	Death	Names	Valid	%	Start	End	Spp/yr	Pubs	Age	Years worked	Pubs/ year
Alexander	1889	1981	11144	10711	0.96	1910	1981	154.8	1017	92	72	14.1
Walker	1809	1874	3917	2691	0.69	1833	1874	92.6	38	65	42	0.9
Kieffer	1856	1925	3528	3143	0.89	1884	1930	75.1	470	69	47	10.0
Loew	1807	1878	3525	2645	0.75	1840	1880	83.3	219	71	41	5.3
Malloch	1875	1963	3315	2749	0.83	1910	1942	100.2	198	88	33	6.0
Macquart	1778	1855	3207	2028	0.63	1819	1855	85.8	34	77	37	0.9
Rob.-Desv.[1]	1799	1857	2805	1427	0.51	1827	1863	75.81	35	58	37	1.5
Meigen	1764	1845	2699	1738	0.64	1800	1835	75.0	10	81	36	0.3
Curran	1894	1972	2664	1940	0.73	1920	1965	57.9	406	78	46	8.8
Edwards	1888	1940	2531	2320	0.92	1907	1941	72.3	408	52	35	11.7
Becker	1840	1928	2381	1946	0.82	1887	1931	52.9	121	88	45	2.7
Hardy	1914	2002	1867	1783	0.96	1936	2001	28.3	236	88	66	3.6

1. Robineau-Desvoidy

On the productivity of dipterists

All of the top thirteen were specialists on Diptera except for Francis Walker, who also worked on a number of other insect groups [for Walker, only statistics related to his work on Diptera are included]. The earlier systematists, who described large numbers of species, described only a few Diptera: Linnaeus (1707–1778) described some 15,000 species (10,000 plants, 5,000 animals), but only 275 flies; Fabricius (1745–1808) described some 9,776 insects, but only 944 flies (Zimsen, 1964). No living dipterist has described more than 700 species; the closest living dipterist to Hardy is Boris Mamaev (1932–), who described 650 species. The only contemporaneous workers who were close to Hardy in numbers were Ken Spencer (1916–2002; 1,224 names, 132 publications; Spencer, 1992) and Bill Wirth (1916–1994; 1,345 names; 406 publications; Arnaud & Arnaud, 2001). Even the great Willi Hennig (1913–1976) only described 514 species (158 publications).

Overall, more than 4,300 workers have described species of flies, but some 1,500 only described a single species; 3,500 ten or less; and only 329 workers have described 100 species or more. The overall average productivity for all dipterists is 0.2 species described per year per author. The overall average validity rate is 84 percent, that is, 145,239 species divided by 173,843 available names.

The data for the number of available names and taxa are from the BioSystematic Database of World Diptera. While this database is far from being complete, about 96% of the names in secondary sources are now included. So, while the actual figures may differ in future versions, the relative positions of the top thirteen are unlikely to change.

Also, in considering productivity one needs think of longevity. Edwards died very young for a taxonomist, but one might speculate that if he had lived as long as Alexander he clearly would have ranked just after Alexander in overall productivity. Elmo Hardy had long and productive years and will probably be the last person to break into the top thirteen.

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